**Universidade de Aveiro** Departamento de Ambiente e Ordenamento

**2014**

**PAULA ALEXANDRA AQUINO MAIA**

# REGENERAÇÃO DA VEGETAÇÃO APÓS O FOGO EM PORTUGAL – IMPLICAÇÕES PARA A GESTÃO

# POST-FIRE VEGETATION REGENERATION IN PORTUGAL – IMPLICATIONS FOR MANAGEMENT

**Universidade de Aveiro** Departamento de Ambiente e Ordenamento
**2014**

**PAULA ALEXANDRA AQUINO MAIA**

# REGENERAÇÃO DA VEGETAÇÃO APÓS O FOGO EM PORTUGAL – IMPLICAÇÕES PARA A GESTÃO

# POST-FIRE VEGETATION REGENERATION IN PORTUGAL – IMPLICATIONS FOR MANAGEMENT

Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Ciências e Engenharia do Ambiente, realizada sob a orientação científica do Doutor Jan Jacob Keizer, Investigador Associado do CESAM – Centro Superior de Estudos do Ambiente e do Mar, Departamento de Ambiente e Ordenamento da Universidade de Aveiro, Portugal e co-orientaçao de Juli García Pausas, Investigador no CIDE – Centro de Investigaciones sobre Desertificación, Valência, Espanha.

Tese desenvolvida no quadro do Programa Doutoral em Ciências e Engenharia do Ambiente, com o financiamento de uma bolsa de doutoramento (SFRH/BD/42168/2007) da Fundação para a Ciência e a Tecnologia (FCT) e o apoio dos projectos EROSFIRE II (PTDC/AGR-CFL/70968/2006), e ”FIREREG”(PTDC/AGR-CFL/099420/2008), ambos financiados pela Fundação para a Ciência e a Tecnologia (FCT) e o FSE no âmbito do III Quadro Comunitário de Apoio.

À Alice e a todos os meninos.
Que possam ver o verde em todas as partes.

“Sobre um dos palácios desmoronados […] erguia-se um jovem pinheiro […]

-Isto vai para diante!

exclamou um pica-pau que martelava num tronco e, cheio de satisfação, observava a floresta avançando e o maravilhoso desenvolvimento verde sobre a terra.”

*In* “A Cidade”

“A young pine tree stood over one of the fallen palaces […]

- We’re moving onward!

cried out a woodpecker, who hammered on the trunk of a tree and regarded the growing forest and the glorious green progress on earth with satisfaction.”

*In* “The Town”

Herman Hesse, 1910

**o júri**

presidente

Doutor José Rodrigues Ferreira da Rocha
professor catedrático da Universidade de Aveiro

Doutora Celeste de Oliveira Alves Coelho
professora catedrática da Universidade de Aveiro

Doutor José António Vega Hidalgo
professor associado da Universidade de Vigo

Doutor Paulo Alexandre Martins Fernandes
professor associado da Universidade de Trás-os-Montes e Alto-Douro

Doutor Joaquim Sande Silva
professor adjunto do Instituto Politécnico de Coimbra

Doutor Jan Jacob Keizer
investigador auxiliar da Universidade de Aveiro

**agradecimentos**

Comecei a escrever os agradecimentos num dia em que precisava de ânimo para continuar. A todos, obrigada.

Ao meu supervisor Jacob Keizer que foi professor, tutor, crítico, revisor, colega, ouvinte e amigo. Obrigada pelo apoio, pela confiança e pela liberdade que tive. Obrigada ao Juli Pausas que, de perto e de longe, deu sempre um apoio tão importante, tão certeiro e que foi um investigador crucial no meu "chamamento" para o fogo.

Aos meus colegas, os que por mais próximos me deram alento e inspiração. A Ana, a Maruxa, o Sérgio, a Diana. Estivémos muitos dias no mesmo barco e puxámo-nos uns aos outros pra dentro. Aos que estavam no mesmo barco, mas por qualquer razão não tão perto, obrigada também. Saber que a Raquel, a Sílvia, a Isabel, a Mariana, a Mitas, o JP, a Anne-Karine, a Dalila, a Rita, o Martinho, o Ócar, o Kaveh, a Juliana …todos os outros que aparecerem e entretanto foram para outros sítios (a princesa Isabelitas!), andavam por perto, deu-me força e amparo.

Aos que me acolheram em Valência. Obrigada ao Bruno, Santí, Clara, Diana, Ana, e todos os outros pela ajuda, convívio e conforto de chegar a um sítio onde não se é uma estranha.

Aos meus pais, que desde sempre fizeram tudo por mim, me ajudaram directa e indirectamente nos vários passos que levaram até este outro passo.

À minha filha Alice, que, mesmo sem o saber, me deu, deste dentro (literalmente) força e vontade para fazer grande parte destas coisas. Que depois de vir cá pra fora, me lembrava todos os dias e todas as horas que a vida tem tantas coisas boas.

Ao Jorge, que não só me deu a força e persistência como exemplo, mas mais me deu o ânimo para fazer mais uma forcinha e aturou as minhas crises existenciais. Obrigada por teres estado sempre comigo.

**palavras-chave**

Fogos florestais, *Pinus pinaster*, matos, *Erica australis*, *Erica umbellata*, *Pterospartum tridentatum*, banco de sementes, severidade do fogo, espécies rebrotadoras, espécies germinadoras, gestão pós-fogo.

**resumo**

Este trabalho pretende aprofundar o conhecimento da regeneração da vegetação após o fogo. Desta forma, pretende contribuir para uma gestão florestal em que a previsão do potencial de regeneração dos ecossistemas seja considerada. Para tal, foram estudados ecossistemas florestais e matos, após incêndios florestais e fogos experimentais.

Estudou-se o efeito da severidade do fogo no recrutamento de *Pinus pinaster* (pinheiro-bravo). Observou-se que a severidade do fogo é essencial neste processo, e que poed ser facilmente inferida pelo grau de dano causado pelo fogo nas copas das árvores. A alta severidade nas copas leva à combustão das pinhas, inviabilizando o banco de sementes e, portanto, o recrutamento pós fogo. No entanto, a severidade do fogo nas copas influencia também as condições locais ao nível do solo, uma vez que a combustão das pinhas leva à diminuição da deposição de agulhas no solo. Com baixa severidade (copas apenas chamuscadas e não queimadas), observou-se uma queda de agulhas considerável, acompanhada de maior densidade de germinação de pinheiros.

O fogo aumentou a germinação do banco de sementes do solo de uma floresta de *Pinus pinaster*, este efeito esteve relacionado com a severidade do fogo. A densidade de germinação dos principais *taxa* (género *Erica* e *Calluna vulgaris*) foi afectada de forma contrastante, dependendo da severidade do fogo, estimada pelo grau de dano nas copas (LCC/HCC), mas também pelo índice baseado no diâmetro dos raminhos queimados (TSI). Nas áreas de baixa severidade houve um aumento na germinação do banco de sementes, enquando que sob alta severidade houve uma diminuição.

A ocorrência de um fogo experimental, num urzal dominado por *Pterospartum tridentatum*, *Erica australis* e *E. umbellata*, não provocou diferenças no número total de plântulas emergidas do banco de sementes. No entanto, esta falta de diferenças resultou da heterogeneidade de temperaturas atingidas pelo fogo ao longo da parcela experimental, o que causou efeitos opostos em termos de mortalidade/estímulo da germinação, especialmente para *E. australis*. Nas amostras que sofreram temperaturas entre 29 e 42.5ºC observou-se um aumento progressivo na densidade de germinação, sendo que o oposto se observou nas parcelas em que as temperaturas variaram entre 51.5 e 74.5ºC. Neste urzal, a densidade de sementes das duas espécies de urze (*E. australis* e *E. umbellata*) foi mais elevada d

A regeneração do sub-coberto de pinhais e eucaliptais, 5 a 6 anos após o último fogo, foi intimamente associada às práticas de gestão florestal pós fogo. A influência do tipo de floresta foi comparativamente insignificante. A mobilização do solo, o corte de árvores e o desbaste da vegetação arbustiva, pós fogo foram associados a uma perda na cobertura vegetal do solo. Todas estas práticas afectaram negativamente o coberto de espécies rebrotadoras, enquanto que as espécies germinadoras não foram afectadas pela mobilização do solo. Foi identificada uma forte influência das regiões biogeográficas nos padrões de regeneração do sub-coberto destas florestas, sugerindo que regiões mais vulneráveis podem sofrer maiores efeitos da gestão, mesmo sob menores pressões do que regiões mais produtivas. Isto evidencia a necessidade de adequar as práticas de gestão florestal à região onde se pretendem efectuar.

**keywords**

Forest fires, *Pinus pinaster*, heathlands, *Erica australis*, *Erica umbellata*, *Pterospartum tridentatum*, seed bank, fire severity, resprouters, seeders, post-fire management

**abstract**

This thesis aims at improving the knowledge on the post-fire vegetation regeneration. For that, forests and shrublands were studied, after forest fires and experimental fires.

Maritime Pine (*Pinus pinaster*) recruitment after fire was studied. Fire severity was evidenced as a major effect on this process. High crown fire severity can combust the pines, destroying the seed bank and impeding post fire pine recruitment. However, crown combustion also influences the post-fire conditions on the soil surface, since high crown combustion (HCC) will decrease the post-fire needle cast. After low crown combustion (LCC) (scorched rather than torched crowns), a considerable needle cover was observed, along with a higher density of pine seedlings. The overall trends of post-fire recruitment among LCC and HCC areas could be significantly attributed to cover by needles, as well by the estimation of fire severity using the diameters of the burned twigs (TSI).

Fire increased the germination from the soil seed bank of a *Pinus pinaster* forest, and the effects were also related with fire severity. The densities of seedlings of the dominant *taxa* (genus *Erica* and *Calluna vulgaris*) were contrastingly affected in relation to the unburned situation, depending on fire severity, as estimated from the degree of fire-induced crown damage (LCC/HCC), as well as using a severity index based on the diameters of remaining twigs (TSI). Low severity patches had an increase in germination density relatively to the control, while high severity patches suffered a reduction.

After an experimental fire in a heathland dominated by *Pterospartum tridentatum*, *Erica australis* and *E. umbellata*, no net differences in seedling emergence were observed, in relation to the pre-fire situation. However, rather than having no effect, the heterogeneity of temperatures caused by fire promoted caused divergent effects over the burned plot in terms of *Erica australis* germination – a progressive increased was observed in the plots were maximum temperature recorded ranged from 29 to 42.5ºC and decreased in plots with maximum temperature ranging from 51.5 to 74.5ºC. In this heathland, the seed density of two of the main species (*E. australis* and *E. umbellata*) was higher under their canopies, but the same was not true for *P. tridentatum*.

The understory regeneration in pine and eucalypt stands, 5 to 6 years post fire, has been strongly associated with post-fire management practices. The effect of forest type was, comparatively, insignificant. Soil tilling, tree harvesting and shrub clearance, were linked to lower soil cover percentages. However, while all these management operations negatively affected the cover of resprouters, seeders were not affected by soil tilling. A strong influence of biogeographic region was identified, suggesting that more vulnerable regions may suffer higher effects of management, even under comparatively lower management pressure than more productive regions. This emphasizes the need to adequate post-fire management techniques to the target regions.

**Contents**

**List of Figures**

**List of Tables**

**List of Abbreviations**

**BTR –** Burnt Trunk Ratio

**EAU** – Erica australis

**EUM-** Erica umbellata

**FCC –** Full Crown Consumption (used as percentage)

**HCC** – Low Crwon Consumption (used as degree of consumption)

**LCC** – Low Crown Consumption (used as degree of consumption)

**MTR** – Maximum Temperature Reached

**NIR** – Near Infrared Spectroscopy

**Nmed** – North Mediterranean

**PTR** – Pterospartum tridentatum

**R** – Resprouter species (including facultative resprouters)

**S** – Seeder species (obligate)

**Smed** – South Mediterranean

**TDI-** Twig Diameter Index (synonym of TSI)

**TSI** – Twig Severity Index (synonym of TDI)

# Chapter 1

# Introduction

# Chapter 1

# Introduction

## 1.1. Fire in the Mediterranean and plant regeneration mechanisms

Fire has exerted pressure in plant communities of Mediterranean region since the early vegetation colonization of terrestrial habitats ( Pausas and Keeley 2009). As a result, many species of fire prone environment present adaptive traits that allow them to persist and regenerate after fires ( Keeley et al. 2011).

There are two basic distinct processes that plants use to cope with fire, at the individual or population level. The ability to regenerate vegetatively from buds located in the underground or above ground organs, allows plants to rapidly recover their photosynthetic ability and survive, at the individual level. These species are called post-fire resprouters. Post-fire seeders have the ability to recruit after fire, from seeds that survive or are stimulated by fire. These two basic regeneration mechanisms can occur exclusively, that is, species can be either obligate seeders or obligate resprouters, but there are species with both traits (facultative resprouters) and several degrees of expression are known (Paula et al. 2009).

Resprouting is a strategy that requires storage of carbohydrates in the roots. These reserves are mobilized for supporting initial growth of the photosynthetic tissues (Paula & Ojeda 2009). The regeneration of obligate seeders is dependent on the ability to produce seeds that either tolerate high temperatures or remain protected from the extreme temperatures of fire on the soil or on the canopy. Post-fire germination from the seed bank can be explained by heat insulation, by heat tolerance, or fire related stimulation (Paula & Pausas 2008) as well as by exposure to chemical triggers related to the combustion of biomass (Moreira et al. 2010).

It is know that post-fire persistence mechanisms are negatively correlated in the Mediterranean Basin flora, it is, that there is a *tradeoff* between the ability to resprout and recruit after fire (e.g. Paula and Pausas 2008; Pausas and Verdu 2005). The common generalization of this relation is that 1) post-fire seeders allocate more energy to produce seeds than resprouters, whose energy investment goes mostly to storing carbohydrate reserves in underground organs (e.g.PATE et al. 1990; Vergaduer and Ojeda 2002) ; 2) seeders produce more seeds, promoting more prolific recruitment than resprouters (Lamont & Wiens 2003).

Contrasting post-fire regeneration strategies imply divergent consequences for the persistence of populations. Post-fire resprouters, by persisting at the individual level typically constitute stable populations, with long lived individuals; on the opposite side, post-fire seeders do not survive fires and entire populations can be replaced by a single fire event (Ojeda et al. 2005; BRADSTOCK 1990; Bond & Midgley 2001). The third generalization that follows is that genetic diversification may be higher among seeders than resprouters (e.g. Lamont and Wiens 2003).

Although some obligate seeders are 'gap recruiters' (Keeley, 1998), and have the ability to recruit between fires, for others the recruitment is mostly concentrated in post-fire periods (Ooi et al. 2006; Wills & Read 2002, 2007). In any of the cases, fire can threat the persistence of seeder populations if the pre-disturbance population is to small (Yates & Ladd 2010), or if the fire-recurrence interval does not allow the formation of a sufficiently large seed bank – 'immaturity risk' (Odion and Tyler 2002, Moya et al. 2008 ab).

## 1.2. Portuguese forests and heathlands - fire and management as disturbances

Despite the fact that fire is now recognized as a natural disturbance, that shaped the vegetation of Mediterranean ecosystems, present fire regimes are not driven by natural

processes, unlike what happened in the past (Pausas et al, 2008). In Portugal, the increase in fire frequency i is part of a cycle that began with a widespread rural exodus (Hespanha 1996), and that is currently expressed in a dramatic change in land use and forest composition. The area covered by maritime pine and blue gum eucalypt, mostly as monospecific plantations, amounts to close to 50% of the country's forested area (ICNF 2013).

The post-fire regeneration of most Mediterranean pines, like *Pinus pinaster* (Ait.) is exclusively dependent on germination (Tapias et al. 2004). Pine seeds do not persist in the soil and have limited ability to resist the high temperatures caused by fire (Escudero et al. 1999; Alvarez et al. 2007). Therefore, most of the post-fire recruitment comes from seeds stored in cones that remain closed after seed maturation and are opened after the passage of fire – serotinous cones (Vega et al. 2008a; Moya, et al. 2008). *Pinus pinaster* is recognised as a serotinous species, however the inter-population variability in the degree of cone serotiny of this species is outstanding, particularly when comparing with other Mediterranean pine species like *Pinus halepensis* (Tapias et al. 2001; Raul Tapias et al. 2004). As a consequence of this, many populations of *Pinus pinaster* may present a very limited potential to self-regenerate after fire. The risk of low – or lack of – post-fire regeneration of pines increases with increasing fire recurrency. High fire recurrency, particularly if return interval is lower than the age required for achieving sexual maturity, potentially results in very low or nill pine regeneration. In fact, low post-fire pine regeneration in some regions, particularly under severe fire regimes is one of the reasons behind the plantation of large areas of *Eucalyptus globulus* (Labill.) (Silva et al. 2011). *E. globulus* is an exotic, fast-growing species with conspicuous vegetative regeneration after fire and after coppicing.

Far from being natural habitats, these highly anthropogenic forests are often cleared and tilled for diminishing competition with the trees, to prepare the ground for planting or to decrease fire risk. The understory vegetation is, according to Bengtsson et al.

(2000), the best indicator of overall biodiversity and, thereby, ecological sustainability of mono-specific plantations. In view of this, intensive management of the understory, may carry severe consequences from the perspective of ecosystem resilience, and the maintenance of ecosystem services provision (Bengtsson et al. 2000). Ecosystem resilience is of particular relevance for fire-prone forests such as pine and eucalypt plantations, as fire frequency in Portugal is not expected to reduce substantially in the near future (Fernandes et al. 2013; Moreira et al. 2011).

Heathlands and other shrublands in the Mediterranean Basin have mostly originated from a variety of disturbances on different pre-existing ecosystems (Calvo et al. 2012; Hufkens et al. 2010). The recurrent pressure posed by fires and wood extraction on forests is in the origin of most shrublands across Europe (Calvo et al. 2012). However, in the Iberian Peninsula, and in particular, in Portugal, most heathlands originate from progressive shrub colonization of abandoned agricultural fields (Moreira et al. 2001).

Despite being mostly considered as marginal and unproductive lands, Mediterranean heathlands are among others, important areas of plant and animal diversity conservation and refuge (namely for pollinators), soil protection, aesthetical and cultural valorisation (PSRNatura 2000; e.g. habitat 4030).

Species like *Erica australis* and *Pterospartum tridentatum*, which are characteristic of heathlands in Central Portugal and North of Spain are strong resprouters that often rapidly regenerate after fire (Fernández et al. 2013; Fernández-Abascal et al. 2004). These two species also present ability to germinate from the soil seed bank after a fire, this is, they are facultative rather than obligate resprouters (Paula & Pausas 2008). Other species characteristic of heathland communities, like *Erica umbellata*, *Calluna vulgaris* and some species of the Cistaceae family are obligate seeders (Paula & Pausas 2008), so the persistence of their populations after a fire is directly dependent on the ability to create a viable seed bank. However, these species differ in terms of the relation of their germination response with fire stimulation.

Studies of the post-fire regeneration of Mediterranean heathlands composed by species with these contrasting regeneration strategies – (facultative) resprouters and obligate seeders – commonly report a rapid post-fire increase in the cover attained by resprouters. The cover of seeders takes longer to attain its original values (Vallejo & Alloza 2012, 1998), or does not reach the pre-fire values at all, especially when post-fire mortality is high due to low water availability (Rego et al. 1991; Quintana et al. 2004). Moreover, the contribution of seedlings from facultative resprouter species is frequently negligible, particularly in comparison with the conspicuous regeneration achieved by resprouting of the same species (Céspedes et al. 2013) .

However, the relation between the soil seed bank and the mother plant may be very strong in species with short distance seed dispersal, and also in dense communities.

Even though fire has helped shaping the characteristics of these communities, high fire recurrence is now considered a threat to the maintenance of these ecosystems (Calvo et al. 2012; Aguiar & Capelo 2000). Recurrent fires may be a threat by the potential to progressively displace species with lower post-fire regeneration ability relatively to prolific post-fire seeders (like some invasive species) or vigorous post-fire resprouters. Conservation of biodiversity is increasingly relevant, also from an economic point of view. Maintaining high plant diversity, even in mono-specific plantations, allows for the exploration of non-wood goods (honey, plant harvesting for multiple purposes) and it represents an important aspect in internationally recognized forest certification schemes such as FSC-STD-01-001 V4-0 EN which in turn, results in the valorization of products resulting from sustainably managed forests.

### 1.3. Fire severity assessment – implications for management of burnt areas

Fire does not behave homogeneously along the landscape; recently burnt areas generally comprise a mosaic of patches that suffered heterogeneous fire severity (Otto et al. 2009; Pausas et al. 2003; Ubeda, et al. 2006). The term severity is here used as

the degree of above ground biomass loss caused by fire, which may be related to the temperature achieved during fire, and hence, of fire intensity ( Keeley 2009).

Fire severity can be inferred from measures that estimate the loss of above-groung biomass. Depending on the needs, such measures may focus on the amount of litter and duff consumed (Fonturbel et al. 2011), ash color (Pereira et al. 2010) , volume of canopy loss (Vega et al. 2008b) or the diameter of remaining branches (Pérez & Moreno 1998). Measures of fire severity can be significant predictors of ecosystem responses such as species richness, patterns of seedling recruitment or forest regeneration (Keeley 2009).

There is a clear applicability of fire severity estimates, as predictors of regeneration, in planning post-fire management operations. The identification of areas with different expected post fire responses – e.g. in terms of tree regeneration or loss of endangered species - could be used for targeting these areas for specific actions – e.g. planting trees for wood production, or seeding for habitat restoration. The planned distribution of management efforts in such a way would allow, not only decreasing expenses while taking profit of natural regeneration as also, not less importantly, to avoid pressures posed by unnecessary management operations (Fischer et al. 2006; Lindenmayer et al. 2006).

### 1.4. Thesis structure and Objectives

This thesis includes four experimental chapters that deal with the effects of fire and post-fire management on the vegetation. The underlying objective, of all the experiments is to further the understanding of the effects of fire (severity) in the responses of the ecosystem, to better predict post fire ecosystem dynamics and contribute to the planning of management actions.

**Table 1** summarizes the research papers, in terms of **1)** the type of fire studied (wildfire or experimental fire), **2)** the component of the vegetation studied (soil seed bank, canopy seed bank - pine recruitment – and understory standing vegetation), **3)** the spatial scale analyzed – from plot scale to regional scale), **4)** the weight of post-fire management on the ecosystem responses studied.

**Table 1** - Outline of the thesis, considering the time and spatial scope of the chapters.

| Spatial scale | Time scale - post fire | | | Ecosystem | (E)xperimental or (F)orest Fire | Fire Severity | Post-fire Management | Vegetation component studied | Main response |
|---|---|---|---|---|---|---|---|---|---|
| | Immediate | Short-term (up to 3 years) | Mid-term (up to 7 years) | | | | | | |
| **Plot** | Chapter 4 | | | heathland | E | x | | soil seed bank | germination from pre-fire (or unburnt) samples *vs.* post-fire germination |
| **Slope** | Chapter 3 | | | pine forest | F | x | | | |
| | | Chapter 2 | | pine forest | F | x | x | pine recruitment | recruitment after fire and salvage logging |
| **Regional** | | | Chapter 5 | pine/ eucalypt plantations | F | | x | understory vegetation | richness and cover after fire and management |

**Chapter 2** presents a field study of the post-fire regeneration of *Pinus pinaster* (Ait.). The main objective of this study was to evaluate to what extent the post-fire pine recruitment and growth after a wildfire was related to fire severity (**Objective 1**). Fire severity was approached in a hierarchical manner. Large sections of the slope were categorized in terms of the consumption of pine tree canopies, and different fire severity indices were done in the plots established in each of the sections. These indices were done by means of measurements of fire damage on different parts of the vegetation. The use of different, but complementary fire-severity indices and local conditions (ash, litter cover estimates) had the objective of comparing their effectiveness for estimating post-fire pine regeneration, and hence, their potential use as tools for post-fire management planning (**Objective 2**). During the experiment, post-

fire operations began to be implemented for pest control, so the responses studies also included the effect of post-fire logging, as a source of temporal variability in pine seedling establishment.

**Chapter 3** was an experimental work dealing with the effects of a wildfire on the soil seed bank of a *P. pinaster* forest. This study was done on the same area and using the same experimental set up as **Chapter 2**, therefore providing a wide evaluation of the community regeneration ability.

The study's specific objective was to evaluate the effects of the fire on the soil seed bank, in terms of seed density and species composition, assessing in which extent these effects were related to fire severity (**Objective 3**). Fire severity was assessed hierarchically, as in **Chapter 2**, but this time, the plot-wise indices also included the estimation of Maximum Temperature Reached (MTR) during fire, by means of Near Infrared Spectroscopy (NIR). MTR was used as a surrogate of fire intensity in the soil, thereby expected to be a more accurate predictor of the post fire soil seed bank germination than the above ground metrics of plant combustion. This way, the effectiveness of the several severity/intensity estimations in predicting the post-fire germination from the soil seed bank was also evaluated (**Objective 4**).

**Chapter 4** analyses the effect of fire in the germination from the soil seed bank using repeated samples before and after an experimental fire conducted on a heathland. This chapter had the main objective of analyzing the importance of the pre-fire soil seed bank in determining the post-fire germination (**Objective 5**). To this end, sampling points equipped with thermocouples were distributed along the experimental area in a grid-like manner. Moreover, the different samples in each sampling point were attributed to each of the three dominant species in the community (*Pterospartum tridentatum*, *Erica australis* and *Erica umbellata*), in order to assess the fine scale patterns of seed deposition in relation to the canopy species (**Objective 6**). Since these

three species have contrasting post-fire regeneration strategies (*E. australis* and *P. tridentatum* are facultative resprouters while *E. umbellata* is an obligate seeder), special focus was given to the post-fire potential persistence of *E. umbellata* in the community, as inferred from the germination from the soil seed bank samples (**Objective 7**).

**Chapter 5** was a study that focused on the mid-term regeneration of the understory community of pure and mixed plantations of *P.pinaster* and *E. globulus*. The main goal was to evaluate the importance of biogeography, topography, forest type and common post-fire management practices on the richness and abundance of woody species (**Objective 8**). To this end, 284 sampling plots, in four biogeographic regions, were sampled between the 2010 winter and 2012 late spring, corresponding to 5 to 7 years after fire. The effects of topography, forest type and post-fire management operations were also analysed for each of the four biogeographic regions, to evaluate regional differences in the richness and abundance of the woody species after fire and post-fire management (**Objective 9**).

**References**

Aguiar, C. & Capelo, J., 2000. Plano Sectorial da Rede Natura 2000 - habitats naturais.

Alvarez, R., Valbuena, L. & Calvo, L., 2007. Effect of high temperatures on seed germination and seedling survival in three pine species (Pinus pinaster, P-sylvestris and P-nigra). International Journal of Wildland Fire, 16(1), pp.63–70.

Bengtsson, J. et al., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management, 132(1), pp.39–50.

Bond, W.J. & Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology & Evolution, 16(1), pp.45–51.

BRADSTOCK, R.A., 1990. Demography of woody plants in relation to fire: Banksia serrata Lf. and Isopogon anemonifolius (Salisb.) Knight. Australian Journal of Ecology, 15(1), pp.117–132.

Calvo, L. et al., 2012. Post-Fire Management of Shrublands. In F. Moreira et al., eds. Post-Fire Management and Restoration of Southern European Forests. Managing Forest Ecosystems. Dordrecht: Springer Netherlands, pp. 293–319.

Calvo, L., Tarrega, R. & Luis, E., 2002. Regeneration patterns in a Calluna vulgaris heathland in the Cantabrian mountains (NW Spain): effects of burning, cutting and ploughing. Acta Oecologica, 23(2), pp.81–90.

Céspedes, B. et al., 2013. Burning season effects on the short-term post-fire vegetation dynamics of a Mediterranean heathland T. O'Connor, ed. Applied Vegetation Science, p.n/a–n/a.

Escudero, A. et al., 1999. Probability of germination after heat treatment of native Spanish pines. Annals of Forest Science, 56(6), pp.511–520.

Fernandes, P.M. et al., 2013. Prescribed burning in southern Europe: developing fire management in a dynamic landscape. Frontiers in Ecology and the Environment, 11(s1), pp.e4–e14.

Fernández, C., Vega, J. a & Fonturbel, T., 2013. Shrub resprouting response after fuel reduction treatments: comparison of prescribed burning, clearing and mastication. Journal of environmental management, 117, pp.235–41.

Fernández-Abascal, I., Tárrega, R. & Luis-Calabuig, E., 2004. Ten years of recovery after experimental fire in a heathland: effects of sowing native species. Forest Ecology and Management, 203(1-3), pp.147–156.

Fischer, J., Lindenmayer, D.B. & Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment, 4(2), pp.80–86.

Fonturbel, M.T. et al., 2011. Effects of soil burn severity on germination and initial establishment of maritime pine seedlings, under greenhouse conditions, in two contrasting experimentally burned soils. International Journal of Wildland Fire, 20(2), pp.209–222.

Hespanha, P., 1996. The Dynamics of Globalization Social Crisis and Conflict in the Portuguese areas.

Hufkens, K. et al., 2010. Habitat reporting of a heathland site: Classification probabilities as additional information, a case study. Ecological Informatics, 5(4), pp.248–255.

ICNF, 2013. Instituto da Conservação da Natureza e das Florestas. Available at: http://www.icnf.pt/portal/florestas.

Keeley, J., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire, 18(1), p.116.

Keeley, J.E. et al., 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science, 16(8), pp.406–411.

Lamont, B.B. & Wiens, D., 2003. Are seed set and speciation rates always low among species that resprout after fire , and why ? , pp.277–292.

Lindenmayer, D.B., Franklin, J.F. & Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation, 131(3), pp.433–445.

Maren, I.E. et al., 2010. Prescribed burning of northern heathlands: Calluna vulgaris germination cues and seed-bank dynamics. Plant Ecology, 207(2), pp.245–256.

Moreira, B. et al., 2010. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. Annals of Botany, 105(4), pp.627–635.

Moreira, F. et al., 2011. Landscape - wildfire interactions in southern Europe: Implications for landscape management. Journal of Environmental Management, 92(10), pp.2389–2402.

Moreira, F., Rego, F.C. & Ferreira, P.G., 2001. Temporal ( 1958 – 1995 ) pattern of change in a cultural landscape of northwestern Portugal : implications for fire occurrence. , 2(Ccrn 1995), pp.557–567.

Moya, D. et al., 2008. Natural post-fire dynamics and serotiny in 10-year-old Pinus halepensis Mill. stands along a geographic gradient. International Journal of Wildland Fire, 17(2), pp.287–292.

Odion, D. & Tyler, C., 2002. Are long fire-free periods needed to maintain the endangered, fire-recruiting shrub Arctostaphylos morroensis(Ericaceae)? Conservation Ecology, 6(2).

Ojeda, F., Brun, F.G. & Vergara, J.J., 2005. Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. The New phytologist, 168(1), pp.155–65.

Ooi, M.K.J., Whelan, R.J. & Auld, T.D., 2006. Persistence of obligate-seeding species at the population scale: effects of fire intensity, fire patchiness and long fire-free intervals. International Journal of Wildland Fire, 15(2), pp.261–269.

Otto, R. et al., 2009. The effect of fire severity on first-year seedling establishment in a Pinus canariensis forest on Tenerife, Canary Islands. European Journal of Forest Research, 129(4), pp.499–508.

Pate, J. et al., 1990. Seedling Growth and Storage Characteristics of Seeder and Resprouter Species of Mediterranean-type Ecosystems of S. W. Australia. Annals of Botany, 65(6), pp.585–601.

Paula, S. et al., 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology, 90(5).

Paula, S. & Ojeda, F., 2009. Belowground starch consumption after recurrent severe disturbance in three resprouter species of the genus Erica. Botany, 87(3), pp.253–259.

Paula, S. & Pausas, J.G., 2008. Burning seeds: germinative response to heat treatments in relation to resprouting ability. Journal of Ecology, 96(3), pp.543–552.

Pausas, J.G. et al., 2003. Fire severity and seedling establishment in Pinus halepensis woodlands, eastern Iberian Peninsula. Plant Ecology, 169(2), pp.205–213.

Pausas, J.G. & Keeley, J.E., 2009. A Burning Story: The Role of Fire in the History of Life. BioScience, 59(7), pp.593–601.

Pausas, J.G. & Verdu, M., 2005. Plant persistence traits in fire-prone ecosystems of the Mediterranean basin: a phylogenetic approach. Oikos, 109(1), pp.196–202.

Pereira, P., Úbeda, X. & Baltrėnaitė, E., 2010. Mapping total nitrogen in ash after a wildland fire: a microplot analysis. Ekologija, 56(3), pp.144–152.

Pérez, B. & Moreno, J.M., 1998. Methods for quantifying fire severity in shrubland-fires. Plant Ecology, 139, pp.91–101.

Quintana, R. et al., 2004. Time of germination and establishment success after fire of three obligate seeders in a Mediterranean shrubland of central Spain. , pp.241–249.

Rego, F.C., Bunting, S.C. & Silva, J.M., 1991. Changes in understory vegetation following prescribed fire in maritime pine forests Forest Ecology and Management. 41(520), pp.21–31.

Silva, J.S. et al., 2011. Wildfires as a major driver of landscape dynamics in three fire-prone areas of Portugal. Landscape and Urban Planning, 101(4), pp.349–358.

Tapias, R. et al., 2001. Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between Pinus halepensis Mill., P. pinaster Ait., P. nigra Arn. and P. pinea L. Journal of Ecology, 89, pp.629–638.

Tapias, R. et al., 2004. Life histories of Mediterranean pines. Plant Ecology, 171(1-2), pp.53–68.

Tapias, R., Pardos, J.A. & Gil, L., 2004. Life histories of Mediterranean pines. Plant Ecology, (171), pp.53–68.

Ubeda, X., Outeiro, L.R. & Sala, M., 2006. Vegetation regrowth after a differential intensity forest fire in a Mediterranean environment, northeast Spain. Land Degradation & Development, 17(4), pp.429–440.

Vallejo, R. & Alloza, J.A., 1998. The restoration of burned lands: the case of eastern Spain. In Large Forest Fires. pp. 91–108.

Vallejo, V.R. & Alloza, J.A., 2012. Post-Fire Management in the Mediterranean Basin. Israel Journal of Ecology & Evolution, 58, pp.251–264.

Vega, J. a. et al., 2009. Response of maritime pine (Pinus pinaster Ait.) recruitment to fire severity and post-fire management in a coastal burned area in Galicia (NW Spain). Plant Ecology, 206(2), pp.297–308.

Vega, J.A. et al., 2008a. The influence of fire severity, serotiny, and post-fire management on Pinus pinaster Ait. recruitment in three burnt areas in Galicia (NW Spain). Forest Ecology and Management, 256(9), pp.1596–1603.

Vega, J.A. et al., 2008b. The influence of fire severity, serotiny, and post-fire management on Pinus pinaster Ait. recruitment in three burnt areas in Galicia (NW Spain). Forest Ecology and Management, 256(9), pp.1596–1603.

Vergaduer, D. & Ojeda, F., 2002. Root starch storage and allocation patterns in seeder and resprouter seedlings of two Cape Erica (Ericaceae) shrubs. American Journal of Botany, 89(8), pp.1189–1196.

Wills, T.J. & Read, J., 2002. Effects of heat and smoke on germination of soil-stored seed in a south-eastern Australian sand heathland. Australian Journal of Botany, 50(2), pp.197–206.

Wills, T.J. & Read, J., 2007. Soil seed bank dynamics in post-fire heathland succession in south-eastern Australia. Plant Ecology, 190(1), pp.1–12.

Yates, C.J. & Ladd, P.G., 2010. Using population viability analysis to predict the effect of fire on the extinction risk of an endangered shrub Verticordia fimbrilepis subsp fimbrilepis in a fragmented landscape. Plant Ecology, 211(2), pp.305–319.

# Chapter 2

# Fire severity as key factor in post-fire regeneration of *Pinus pinaster* (Ait.) in Central

## Chapter 2

## Fire severity as key factor in post-fire regeneration of *Pinus pinaster* (Ait.) in Central Portugal

This chapter is published as:

Maia, P., Pausas, J. G, Vasques, A. and Keizer, J. J. 2012. Fire severity as key factor in post-fire regeneration of *Pinus pinaster* (Ait.) in Central Portugal. Annals of Forest Sciences. 69(4):489-498.

### Abstract

**Context:** Pine woodlands in the Mediterranean are strongly affected by wildfire but there are important gaps in the current knowledge of post-fire regeneration of *Pinus pinaster* Ait. (Maritime pine), including in relation to the role therein of fire severity.

**Objectives:** The principal research questions were: (i) do post-fire seedling densities of Maritime pine differ between patches where pine canopies were consumed to a low vs. high degree by the wildfire; (ii) which factors, besides fire severity, could explain these differences. **Methods:** Following a wildfire in August 2008 near Colmeal, Central Portugal,, pine recruitment was monitored in 18 25m$^2$ plots, equally divided over two fire severity classes designated as high and low crown consumption. This was done at eight occasions from 2 to 36 months after the wildfire. Besides degree of crown consumption, three quantitative fire-severity indices as well as post-fire site conditions, seed input and understory vegetation recovery were measured.

**Results:** Average pine seedling densities were consistently higher in the plots with low than high crown consumption throughout the study period but, due to marked spatial variability, were only significantly different at two out of eight sampling occasions. The spatial variability in pine seedling density could be explained to a significant extent by fire severity (quantitative index based on the diameter of remaining twigs) as well as by

seed input (density of pine cones within the plots) and post-fire site conditions (covers of litter and of ash).

**Conclusion**: Fire severity was found to play a significant role in the recruitment of Maritime pine following wildfire, both using a qualitative, "quick-and-dirty" severity index as using a quantitative, more labour-intensive one.

**Keywords:** fire severity; *Pinus pinaster*; post-fire regeneration; post-fire site conditions

### 2.1. Introduction

Pine woodlands are one of the Mediterranean Basin's ecosystems that are most affected by wildfires(Pausas et al. 2008), and their post-fire regeneration has been an important focus of scientific research over the past few decades (Pausas et al. 2004; Thanos and Skordilis 1987; Thanos et al*.* 1996; Trabaudet al. 1985). *Pinus halepensis* has been extensively studied in Spain, and it is now well established that the species' canopy seed bank is a key factor in its post-fire regeneration (Eshel et al*.* 2000; Herranz et al*.* 1997; Pausas et al*.* 2003). Whilst *Pinus halepensis* is highly serotinous throughout the Iberian Peninsula (Tapias et al. 2004), *Pinus pinaster* (Maritime pine) reveals marked variation in serotiny as well as in other fire-related characteristics within its geographical range (Barbéro et al*.* 1998; Gil et al. 2009; Tapias et al*.* 2004). Also, post-fire regeneration of *Pinus pinaster* has been studied less extensively than that of *P. halepensis*. Prior studies into post-fire recruitment of *P. pinaster* mainly concerned seed and cone traits as well as germination under controlled conditions (Alvarez et al. 2007; Fonturbel et al. 2011; Madrigal et al*.* 2010; Reyes and Casal 2001, 2004; Torres et al. 2006). The - few - studies that addressed post-fire recruitment of *P. pinaster* under field conditions were carried out in Spain (Calvo et al. 2008; Vega et al. 2008, 2010), notwithstanding the fact that Maritime pine woodlands are the most fire-prone forest type in Portugal (Silva et al. 2009).

Recently burnt areas generally comprise a mosaic of heterogeneous site conditions (Otto et al. 2010; Pausas et al. 2003; Ubeda et al. 2006; Vega et al. 2010), which can be expected to influence post-fire vegetation recovery. A key factor in this spatial variability is often the *in-situ* fire intensity (Otto et al. 2010; Pausas et al. 2003; Vega et al. 2008, 2010), but also other abiotic factors such as pre-fire forest management (Perez and Moreno1998) or topography (Pausas et al. 2004) can play a role. With respect to biotic factors, inter-specific competition by the understory vegetation was found to condition post-fire regeneration of Aleppo Pine populations, even from an early stage of recruitment (De las Heras et al. 2002; Nathan and Ne'eman 2004). In forest management, the understory vegetation is commonly regarded as having a negative impact on pine densities and growth, and is therefore often (partially) eliminated. Nonetheless, positive effects of the understory on post-fire pine recruitment have also been suggested (Calvo et al. 2008; Trabaud et al. 1985).

The main aim of this study was to further the knowledge of the regeneration of Mediterranean pine woodlands following wildfires, in particular that of *Pinus pinaster* stands. The specific objectives were : (1) to quantify seedling recruitment of *Pinus pinaster* during the first 36 months after a wildfire; (2) to assess the role therein of key abiotic and biotic factors, in particular fire severity as evaluated using three distinct vegetation-based indices and recovery of the understory vegetation; (3) to evaluate which of these three severity indices is most appropriate to predict post-fire pine regeneration and, thus, of most interest from a forest management point-of-view.

## 2.2. Materials and Methods

### 2.2.1. Study area

The study area was located in Central Portugal, on the border of the municipalities of Góis and Arganil of the Coimbra District, near the village of Colmeal. A wildfire took place on August 24 2008, burning in total some 60 ha. Within the burnt area, a west-

facing slope of roughly 20 ha covered with *Pinus pinaster* Ait. (40º08' - 45 º77'N, 7º59' - 08º22'W, 468 -525 m a.s.l.) was selected for this study. The study site was selected for revealing a rather homogeneous Maritime pine cover before the wildfire, on the one hand, and, on the other, a markedly heterogeneous fire impact, as suggested by well-defined differences in the consumption of the pine crowns. The pre-fire pine cover was observed on available satellite imagery (GoogleEarth) and aerial photography.

Vegetation relevees carried out in adjacent unburnt patches on the study slope suggested that before the wildfire the understory vegetation was mainly composed of shrubs and grasses, in particular, *Arbutus unedo* L., *Erica australis* L., *Calluna vulgaris* (I.) Hull, *Pterospartum tridentatum (*L.)Willk and *Phyllirea angustifolia* L., and *Agrostis curtisii* Kerguélen and *Agrostis delicatula* Pourr. ex Lapeyr (plant nomenclature following Tutin et al. (1964-1980)). In February 2009, the study site was logged and the felled trunks extracted for reasons of plague prevention. Logging of the sample plots, however, was done with utmost care and provoked no visible disturbance to the recovering vegetation. Various tree-ring counts were carried out of the remaining trunks, indicating that at the time of the wildfire the age of the pine stand was approximately 25 years. The level of serotiny of the stand was estimated by counting the closed and open cones in the canopies of 30 pine trees located immediately outside the burnt area, and computed as the average percentage of closed cones.

The climate of the study area can be classified as Meso-Mediterranean (Rivas-Martínez et al. 2002). The mean annual temperature is estimated to be between 10 and 12.5 $^{o}$C, and the average annual rainfall between 1400 and 1600 mm (APA 2011). Two soil profiles excavated in different parts of the study site suggested that the soils are predominantly shallow Leptosols (WRB 2007), overlying pre-Ordovician schists of the Hercynian Massif (Ferreira 1978).The topsoil (0-5 cm) of these profiles had a sandy loam to loam texture (Santos 2010: sand: 29-54 %; silt: 29%; clay: 16-22 %).

### 2.2.2. Experimental design

The experimental design that was originally envisaged comprised three pairs of nearby transects with easily-observed, contrasting fire severities, in this case evidenced by different degrees of pine crown consumption. Photographs from the opposite side of the valley did allow selecting three zones, where pine crown consumption varied markedly over short distances. Dark-coloured patches were taken to reflect (almost) complete consumption of the pine crowns, whereas light-coloured patches were interpreted to correspond to scorched crowns, retaining substantial amounts of - dead - needles. However, *in-situ* estimation of pine crown consumption (FCC, see underneath) obliged to a re-classification of one of the dark-coloured patches as well as one of the light-coloured patches. Although the resulting experimental design continued balanced, it no longer involved paired transects of High and Low Crown Consumption (HCC and LCC; **Figure 1**).

The six transects were laid out in a perpendicular direction to the contour lines and on basically the same slope positions, so as to minimize differences in topographic and soil conditions. They had a length of approximately 30 m, along which three plots of 25 $m^2$ were established at intervals of roughly 10 m. In turn, each plot was subdivided in four subplots of 2.5 m by 2.5 m, which were separated by corridors of 1 m width to facilitate the monitoring of pine recruitment and vegetation recovery.

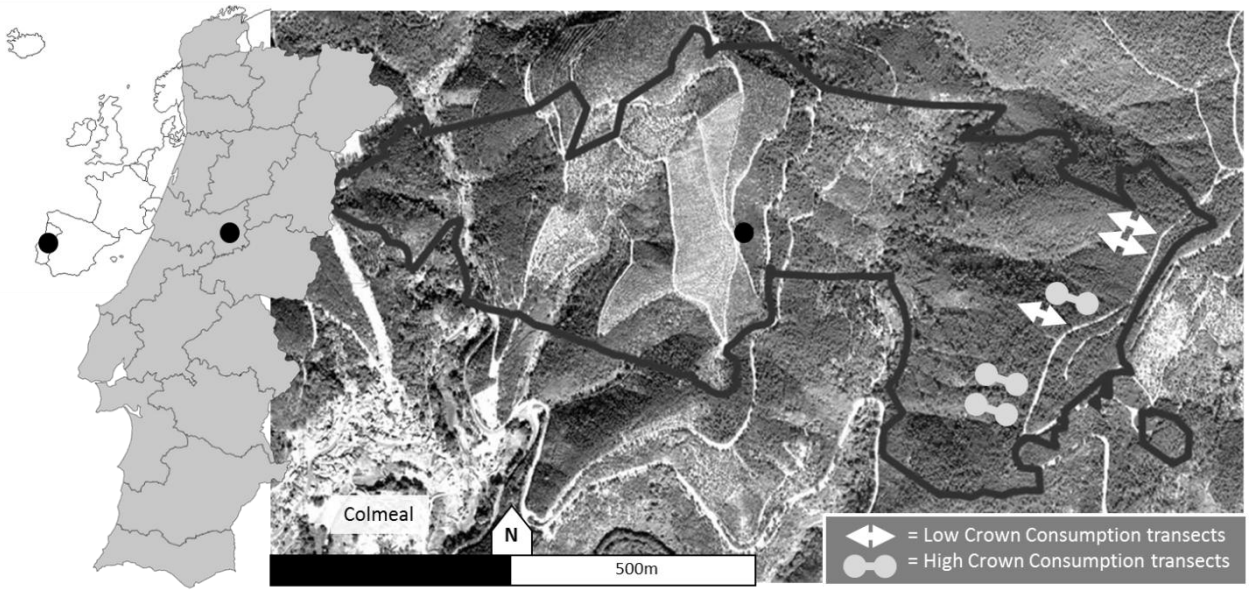



**Figure 1 -** Location of the study area and of the six transects with contrasting fire severities, classified as High and Low Crown Consumption (HCC and LCC) of the Maritime pine trees

.

### 2.2.3. Field measurements

During the first two weeks after the wildfire, the pre-fire stand characteristics at each plot were described by measuring the diameter at breast height (DBH) and height of all standing trees. Simultaneously, fire severity was estimated based on: (i) height of flame marks on the pine trunks, expressed as the average ratio of flame height to total tree height (BurntTRunk, BTR); (ii) number of pine trees whose needles were all consumed by the fire, expressed as fraction of Fully Consumed Crowns (FCC); (iii) diameter of the three thinnest remaining twigs of 5 to 10 randomly selected shrubs within each plot, expressed as ratio of average plot-wise diameter to the maximum value of the twig diameters measured in all 18 plots (Twig Severity Index, TSI). A possible limitation of the TSI was that the selected shrubs were not identified in terms of species (as would have been possible, albeit only at a later stage and just for the surviving shrubs). Finally, the number of pine cones lying on the ground within each plot was counted as

an indicator of pine seed input. This was repeated in March 2009 to account for the impact of the logging. Pine seed input was further estimated by means of seed traps, following the design by Cottrell (2004) and consisting of a funnel with an orifice of 150 $cm^2$ placed at 20 cm above ground level. At each plot, one seed trap was installed within the first three weeks after the wildfire and then monitored for seed rain at regular intervals. During the entire 36-month study period, however, none of the 18 traps caught any Maritime pine seed.

Post-fire pine recruitment was first evaluated two months after the wildfire, in October 2008, and then repeated at seven occasions, with a decreasing frequency with increasing time-since-fire up till the end of this study in August 2011. At each occasion, all green pine seedlings/saplings within each plot were counted; at the last occasion, the saplings' heights were also measured. The October-2008 field campaign further involved estimating the horizontally-projected ground covers of bare soil, ash and litter. This was done visually for each of the four subplots, estimating percentage cover to the nearest integer and then averaging them to arrive at the plot-wise values. The total cover of the understory vegetation (i.e. excluding the pine seedlings/saplings) as well as the cover of the individual plant species was estimated in the same manner but at two later occasions, in March 2010 and August 2011. The predominant mode in which each species regenerated – by resprouting or through germination – was assessed by careful visual inspection.

### 2.2.4. Data analysis

The two crown consumption classes were compared with respect to the observed pre-fire pine stand characteristics as well as the post-fire measurements of fire severity, ground cover, seed input, pine recruitment and understory vegetation recovery. This was done by means of nested ANOVAs, with the plots nested under their respective transects, and using the univariate GLM procedure of SPSS (v.16). SPSS was further

used to assess the agreement between the three fire severity indices, by means of the Spearman rank correlation coefficient. Likewise, the correlations of these indices with the covers of bare soil, ash and litter cover were determined, for the expected association on these site conditions with fire intensity. Finally, the SPSS procedure of univariate GLM regression was employed to determine which of the severity indices and post-fire site conditions could explain a significant part of the observed variation in post-fire vegetation recovery. Such variable(s) could then be applied in post-fire land management as simple predictor of pine recruitment in particular. The GLM regressions involved the same nested design as the ANOVAs.

The statistical analyses were carried out using rank-transformed values rather than the original values (McDonald 2009). This was done because the distributions of the various variables clearly deviated from normal and because a wide range of other transformations did not result in more satisfactory distributions.

## 2.3. Results

### 2.3.1. Fire severity measures and post-fire site conditions

All three fire severity indices presented, on average, noticeably higher values in the High Crown Consumption (HCC) plots than in the Low Crown Consumption (LCC) plots (**Table 2**). This difference was statistically significant in the case of the Burnt Trunk ratio (BTR: $p = 0.03$) and the Twig Severity Index (TWI: $p = 0.03$) but only marginally so in the case of the Fully Consumed Crowns index (FCC: $p = 0.06$), due to a greater variability amongst the HCC plots in particular

The ground covers of bare soil and ash immediately after the fire were, on average, markedly higher in the HCC than LCC plots, whereas the opposite was true for the litter cover (**Table 2**). Litter cover consisted by and large of pine needle cast from scorched

pine crowns, attaining a particularly elevated value at the LCC plots (75 %). The HCC and LCC plots differed significantly in terms of bare soil ($p = 0.01$) and litter cover ($p = 0.04$) but only marginally so in terms of ash cover ($p = 0.07$). This lack of significance reflected the comparatively low cover values of ash, combined with a relatively high spatial variability.

In line with their association with the two crown consumption classes, the three fire severity indices and the three ground cover variables were all strongly and significantly correlated one with each other (

**Table 3**). The correlations between the severity indices, however, were less strong than those between the cover variables ($r_s$= 0.84-0.97 vs. 0.49-0.68). Amongst the three severity indices, TSI was most closely associated with all three of the ground cover variables ($r_s$= 0.74-0.76 vs. 0.59-0.71).

**Table 2** – Mean values, standard deviations and nested ANOVA p-values for the various vegetation, site and fire severity characteristics determined at the nine High and nine Low Crown Consumption plots. The significant differences at α = 0.05 were given in bold.

| | | | Crown Consumption (CC) | | | | nested ANOVA p-value |
|---|---|---|---|---|---|---|---|
| | | | High CC | | LowCC | | |
| | | | Mean | StDev | Mean | StDev | |
| pre-fire stand characteristics | | standing pine trees (nr.m$^{-2}$) | 0.25 | 0.16 | 0.28 | 0.16 | 0.46 |
| | | DBH (cm) | 33 | 5 | 35 | 5 | 0.76 |
| fire severity indices | | FCC | 0.29 | 0.18 | 0.06 | 0.10 | 0.06 |
| | | BTR | 0.99 | 0.00 | 0.77 | 0.29 | **0.03** |
| | | TSI | 0.39 | 0.08 | 0.21 | 0.13 | **0.03** |
| post-fire site conditions (% cover) | | bare soil | 34 | 8 | 8 | 4 | **0.01** |
| | | ash | 46 | 11 | 17 | 20 | 0.07 |
| | | litter | 20 | 19 | 75 | 23 | **0.04** |
| pine seed input (nr cones.m$^{-2}$) | | post-fire | 0.03 | 0.05 | 0.11 | 0.07 | **0.01** |
| | | post-harvest | 0.16 | 0.17 | 0.12 | 0.17 | 0.10 |
| vegetation regeneration | pine seedling/saplings (nr.m$^{-2}$) | 2months | 0.07 | 0.10 | 0.12 | 0.08 | 0.29 |
| | | 18months | 0.58 | 0.43 | 1.39 | 0.71 | 0.07 |
| | | 36months | 0.53 | 0.40 | 1.31 | 0.64 | **0.05** |
| | pine sapling height (cm) | 36months | 71 | 30 | 68 | 13 | 0.61 |
| | understory vegetation cover (%) | reprouting_18months | 7 | 4 | 8 | 6 | 0.96 |
| | | germinating_18months | 6 | 2 | 4 | 3 | **0.01** |
| | | resprouting_36months | 24 | 11 | 28 | 15 | 0.93 |
| | | germinating_36months | 15 | 7 | 16 | 7 | 0.37 |

**Table 3-** Spearman rank correlation coefficients and corresponding p-values for the three fire severity indices and the three descriptors of post-fire site conditions at the 18 study plots. The significant coefficients at α = 0.05 were given in bold.

| | | post-fire site conditions (% ground cover) | | | fire severity indices | |
|---|---|---|---|---|---|---|
| | | bare soil | ash | litter | TSI | BTR |
| fire severity indices | FCC | **0.62** <0.01 | **0.59** 0.01 | **-0.59** 0.01 | **0.49** 0.04 | **0.56** 0.02 |
| | BTR | **0.71** <0.01 | **0.65** <0.01 | **-0.64** <0.01 | **0.68** <0.01 | |
| | TSI | **0.75** <0.01 | **0.74** <0.01 | **-0.76** <0.01 | | |
| post-fire site conditions (% ground cover) | litter | **-0.97** <0.01 | **-0.92** <0.01 | | | |
| | ash | **0.84** <0.01 | | | | |

### 2.3.2. Pine seedling densities

Pine recruitment followed a similar evolution at the HCC and LCC plots (**Figure 2 -** Average densities, and their standard deviations, of *Pinus pinaster* seedlings/saplings at the High and Low Crown Consumption (HCC and LCC) plots along the 36-month study period following the wildfire in August 2008.The two instances of significant differences, at α = 0.05, between the HCC and LCC plots were indicated with an octagonal with “s”.**Figure 2**). Four phases could be identified: (i) an initial increase in pine densities between October 2008 and January 2009; (ii) a decrease between January and March 2008, which was attributed to the logging of the stand in February 2008; (iii) a second increase between March and August 2008; (iv) stable densities between August 2009 and August 2011.

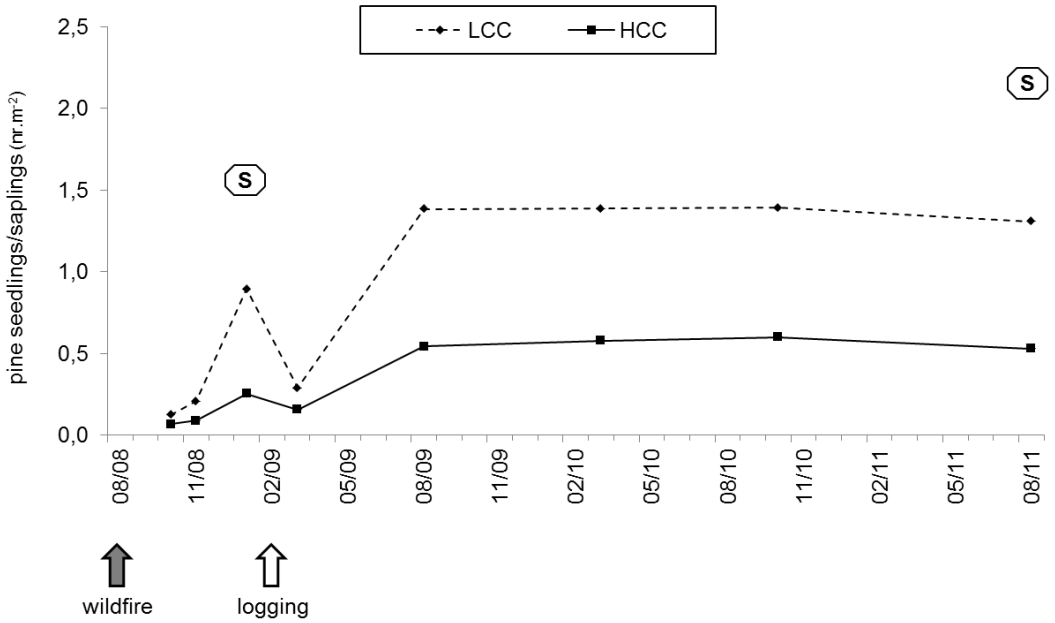



**Figure 2 -** Average densities, and their standard deviations, of *Pinus pinaster* seedlings/saplings at the High and Low Crown Consumption (HCC and LCC) plots along the 36-month study period following the wildfire in August 2008.The two instances of significant differences, at α = 0.05, between the HCC and LCC plots were indicated with an octagonal with "s".

Pine seedling/sapling densities were, on average, consistently higher at the LCC than HCC plots throughout the study period. These differences were statistically significant only at two occasions, i.e. 5 months after the fire in January 2009 and 3 years after the fire in August 2011 (nested ANOVA: p = 0.04 and 0.05, respectively). Nonetheless, they were marginally significant during the entire 4$^{th}$ phase of stable densities from August 2009 onwards, as illustrated for March 2010 in **Table 2**. The lack of significant differences during this final phase was due to the elevated spatial variability in pine recruitment, especially at the HCC plots with coefficients of variation amounting to roughly 75 %.

The spatial variation in pine recruitment could be explained reasonably well by one of the fire severity indices in particular, i.e. TSI (**Table 4**). At three distant periods after the wildfire (2, 18 and 36 months), TSI could account for a fraction of this variation that

was marginally significant (GLM: p = 0.05-0.09). Two of the ground cover variables, however, had a significant effect on pine seedling/sapling densities at all three occasions (**Table 4**). From these two, ash cover consistently revealed a stronger relationship with pine recruitment than litter cover (GLM: p = <0.01-0.01 vs. 0.01-0.04).

**Table 4 -** GLM univariate regression results linking pine recruitment and understory regeneration to fire severity, post-fire site conditions and pine seed input. The significant (at α = 0.05) and marginally significant (α = 0.05-0.10) correlations were indicated by "s" in bold and "~s", respectively, followed by the sign of the correlation coefficient and the p-values.

| | | | | EXPLANATORY VARIABLES | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | fire-severity related | | | | | | pine seed input (nr cones.m$^{-2}$) | |
| | | | | severity indices | | | post-fire soil conditions (% ground cover) | | | | |
| | | | | FCC | BTR | TSI | bare soil | ash | litter | post-fire | post-harv. |
| | vevegation regeneration | pine seedlings/saplings (nr.m-2) | 2months | n.s. | n.s. | ~ s (-) 0.09 | ~ s (-) 0.08 | **s (-) <0.01** | **s (+) 0.04** | n.s. | |
| | | | 18months | n.s. | n.s. | ~ s (-) 0.05 | ~ s (-) 0.06 | **s (-) 0.01** | **s (+) 0.03** | **s (+) 0.02** | n.s. |
| | | | 36months | ~ s (-) 0.09 | n.s. | ~ s (-) 0.06 | **s (-) 0.03** | **s (-) <0.01** | **s (+) 0.01** | **s (+) 0.02** | n.s. |
| | | pine height (cm) | 36months | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | | |
| | | understory vegetation cover (%) | resprouting_36months | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | | |
| | | | germinating_18months | n.s. | **s (+) <0.01** | **s (+) 0.04** | ~ s(+) 0.08 | n.s. | n.s. | | |
| | | | resprouting_36months | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | | |
| | | | germinating_36months | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | | |

### 2.3.3. Pine seed input

Pine cone density could explain the spatial variation in pine recruitment to a significant extent (**Table 4**). This role of pine seed input involved a time lag, however. The pine seedling/sapling densities 18 and 36 months after the wildfire were significantly related to the cone densities in September 2008 (GLM: p's = 0.02) but not to the cone densities in March 2009, after the logging. Also, the seedling/sapling densities 2 months after the wildfire revealed no significant influence of the cone densities immediately after the fire.

The density of pine cones lying on the ground within the plots was, on average, twice as high in March 2009, after the logging, than in September 2008, immediately after the wildfire (0.07 vs. 0.14 cones m-2). This increase, however, was marginal in the case of the LCC plots as opposed to that of the HCC plots (**Table 2**). Whilst the LCC plots contained significantly more cones than the HCC plots in September 2008, they contained markedly less in March 2009, albeit not significantly.

### 2.3.4. Pine sapling heights

Three years after the wildfire, the pine saplings had, on average, attained basically the same height in the HCC and LCC plots, i.e. approximately 70 cm. Like in the case of the pine densities, the HCC plots revealed a greater spatial variability in pine height than the LCC plots (coefficient of variation = 40 vs. 20 %). Sapling height lacked apparent relationships with any of the fire severity indices or immediate post-fire site conditions (**Table 4**), and was also not significantly correlated with the concurrent sapling densities (p = 0.83).

### 2.3.5. Regeneration of the understory vegetation

The regeneration of the understory vegetation 18 and 36 months after the wildfire was similar for the LCC and HCC plots, in terms of: (i) overall covers; (ii) the covers of germinating as well as resprouting species; (iii) the predominance of resprouting over germinating species, particularly at the end of the study period (**Table 2**). The only significant difference was that in the cover of the germinating species in March 2010, being slightly higher in the HCC than LCC plots (6 vs. 4 %). This fact was also evidenced by the GLM results, with two of the fire severity indices explaining a significant fraction of the variation in the March 2010 cover of the germinating species (**Table 4**). There were no clear suggestions that understory regeneration influenced pine recruitment, as covers were not significantly correlated with either pine densities or pine heights (p's = >0.10).

The understory vegetation of the HCC and LCC plots also differed little in species composition (**Supplementary Material 1**). Various species, however, attained markedly different covers in the two types of plots at both sampling occasions. Amongst the resprouting species, *Erica australis* was clearly more abundant in the HCC than LCC plots, whilst the opposite was true for *Pterospartum tridentatum* and *Agrostis curtisii*. Amongst the germinating species, the principal difference was that in *Cistus psilosepalus.*

## 2.4. Discussion

This study revealed marked temporal as well as spatial variation in pine recruitment following a wildfire. Pine densities took approximately one year to reach maximum levels but revealed no major net changes afterwards. Maximum densities could be attained even quicker in the absence of logging, as suggested by the marked die-back in pine seedling between January and March 2009. On the other hand, there was no suggestion of seasonal variation in pine densities, at least during the second year

following wildfire. Seasonal decreases in pine densities were reported by Martínez-Sanchez et al. (1999) but for *Pinus halepensis* and under more arid conditions. Also, pine recruitment in this study did not involve extreme weather conditions (Pausas et al. 2003) or apparent signs of plague attack (Vega et al. 2010).

Fire severity played a significant role in the spatial variability in pine recruitment. This pattern could be captured by the two classes of High and Low Crown Consumption (HCC and LCC), notwithstanding the classification's qualitative and somewhat subjective nature. Possibly, logging masked the association of HCC/LCC with pine densities in two different manners: (i) by provoking more die-back in the LCC than HCC plots; (ii) by enhancing spatial variability in pine densities, especially amongst the LCC plots. This latter effect would seem to be long-lasting, at least 2.5 years (as differences were significant 36 months after the wildfire) and probably even considerably longer (as the coefficients of variation continued high 36 months after the fire).

Amongst the more quantitative proxies of fire severity studied here, litter and ash cover could best explain the spatial variability in pine densities. The relationship of pine densities with these two cover variables was furthermore less susceptible to changes through time than the relationship with HCC/LCC. In the present case, ash and litter cover were almost perfectly correlated and, thus, could be used interchangeably for predicting pine recruitment. Prior studies, however, suggested that an effect of litter cover would be more consensual than one of ash cover. Whilst post-fire soil conditions are widely held to play a key role in the successful germination and early establishment of pines (e.g. Pausas 2003; Madrigal 2010; Vega 2008), litter cover was reported to enhance pine recruitment in various manners, including through the accumulation of seeds, their protection against predators and surface wash, and an increased nutrient availability (Bonnet et al. 2004; Denhamet al. 2009; Fernandez et al. 2008, 2011; Garcia-Fayos and Cerda 1997; Saracino et al. 1997). Ash cover, on the other hand, was found to have, like here, a negative effect on pine density by Ne'eman and Izhaki (1998) as well as by Reyes and Casal (2001, 2004) but a positive effect by

Ne'eman(1997) and Pausas et al. (2003). From a purely practical point-of-view, litter cover would seem easier and quicker to estimate than ash cover. A first estimation of litter cover could then be obtained - even more easily and quickly - by means of the two Crown Consumption classes, as justified by the logical as well as statistical link between litter cover and needle cast from scorched crowns. Prior studies such as Otto et al. (2010), Pausas et al. (2003) and Vega et al. (2010) likewise related heterogeneous site conditions to fire severity classified according to the degree of crown consumption.

Pine recruitment in this study did not seem to be affected by the understory vegetation. This could be due to the low cover attained by the understory vegetation but also to the low density of pine seedlings. The latter would be in line with the findings of Calvo et al. (2008) that the density of pine seedlings was a determining factor for the interespecific competition with the understory species. Pausas et al. (2003), on the other hand, reported that post-fire recruitment of *Pinus halepensis* could be limited by high covers of resprouters, in particular gramineous species. Whilst the cover of the gramineous species in this study was low (HCC plots) to insignificant (LCC plots), inter- and intra-competition could be less intense due to the much less arid conditions than in the case of Pausas et al. (2003).

Pine recruitment was found here to reflect differences in seed input in the form of cones lying on the forest floor immediately after the wildfire. These differences in pine cones were, in turn, associated with fire severity. Apparently, the High Consumption of the Crowns also resulted in more cones being fully combusted than the Low Crown Consumption did. HCC could further have produced a greater mortality in the aerial seed bank than LCC (Reyes and Casal 2002). The effect of pine cone density, however, revealed a clear time lag, suggesting that seed release from the cones mainly occurred in the early stages following wildfire, on the one hand, and, on the other, that the released seeds germinated over a period of at least one year. The importance of

the initial post-fire period for seed release was also indicated by the lack of a significant impact of the changes in pine cone densities that had occurred after logging.

Possibly, the principal release of pine seeds occurred after the cones had been shed from the canopies. Especially in the case of the LCC plots, temperatures might not have increased sufficiently to enable a quick and even seed release (Reyes and Casal 2002). This possibility would seem to agree well with the results of the seed traps, indicating the total absence of pine seed rain, at least from three weeks after the fire onwards. Such a lack of pine seed rain could relate to the timing of the wildfire – having occurred before the end of August, in line with García-Fayos et al. (2001) – in combination with the low level of serotiny of the studied population (20 %). Nonetheless, the number and size of the seedtraps employed here might not have been entirely sufficient (Vega et al. 2010), and should ideally have been installed sooner after the fire  Also, a comparison of the spatial patterns in cone and seedling locations might have shed further light on the timing of seed release.

Pine recruitment three years after the Colmeal wildfire amounted, on average, to 0.9 pine saplings per $m^2$ and in no case exceeded 2.5 saplings per $m^2$.  These figures were well below those reported by Vega et al. (2010: 7 pines per $m^2$) and especially Calvo et al. (2008:12 pines per $m^2$). This could be due to differences in serotiny, Calvo et al. (2008) having studied a highly serotinous population. Although the pine recrutiment densities observed here were low compared to those reported by studies in Spain (Calvo et al. 2008; Vega et al. 2008, 2010), they did cleary exceed  the pre-fire stand densities, i.e. with a factor 2 to 4. They were also substantially higher than the standard densities for 10 year-old pine stands (Oliveira 1999: 1000 to 1500 plants per ha). Thus, except for changes in the observed trend of stable sapling densities after the first post-fire year, pine densities in the study area would, from a forest management point-of-view, need to be thinned out substantially in the next three years (Oliveira 1999), especially in the slope parts where fire severity was lowest.. On the other hand, there was no suggestion of the need for management of the understory vegetation, not only

because of the aforesaid excess of pine saplings but also because of its apparent lack of influence on pine densities as well as sapling height.

### 2.5. Conclusions

Fire severity, as evidenced by degree of crown consumption of the pine trees as well as by various severity indices related to soil surface properties (ash and litter cover) and damage of shrubs (Twig Severity Index), was highlighted as a key factor in post-fire pine recruitment of Maritime pine in Central Portugal. This emphasized the importance of viewing recently burnt areas as heterogeneous rather than homogeneous management units. At the same time, this study demonstrated the potential of simple indices of fire severity for assessing post-fire pine recruitment, even though the need for further testing in other recently burnt areas is more than obvious. Likewise, logging seemed to provoke an important die-back in pine seedlings but the longer-term effects could not be assessed.

Pine recruitment was significantly higher following lower than higher fire severity. This could be attributed first and foremost to a combined effect of less damage to the canopy seed bank and of forest floor conditions more propitious to seedling germination and early establishment. Pine height growth, on the other hand, was not affected by differences in fire severity. The same was *grosso modo* true for the regeneration of understory vegetation, so that there was also no evidence for competition with pine regeneration.

### Acknowledgments

Our thanks go to all those people who, in many ways, helped with the field work, in particular Carli Mertopawiro, RoelToonen, Hein Vermin, Diana Vieira, Helga Fernandes, Isabel Fernandes, and “Polly” Jingxian Tao. We also thank the Portuguese National Forestry Authority (AFN) and the Technical Forestry Office (GTF) of Arganil municipality for their authorization to work in the study area, the GTF of Góis

municipality for the information on the burnt area, and the “Junta de Freguesia” of Colmeal for their logistic support. We finally want to acknowledge the contribution of two anonymous reviewers in improving this manuscript.

**Funding**

P. Maia and A. Vasques were funded through PhD grants attributed by the Portuguese Foundation for Science and Technology (FCT), with references SFRH/BD/42168/2007 and SFRH/BD/47522/2008, respectively. The EROSFIRE II project, which provided logistic support in the bulk of the field campaigns, was also funded by the FCT, with co-funding by FEDER through the POCI2010 Programme (PTDC/AGR-CFL/70968/2006).

**References**

Alvarez R, Valbuena L, Calvo L (2007) Effect of high temperatures on seed germination and seedling survival in three pine species (Pinus pinaster, P-sylvestris and P-nigra). Int J Wildland Fire 16: 63-70

APA (2011) Agência Portuguesa do Ambiente. Accessed November 2011

Barbéro M, Loisel R, Quézel P, Richardson DM, Romane F (1998) Pines of the Mediterranean Basin. In: Richadson DM (Ed), Ecology and Biogeography of Pinus. Cambridge University Press, Cambridge, pp 3-46

Calvo L, Santalla S, Valbuena L, Marcos E, Tarrega R, Luis-Calabuig E (2008) Post-fire natural regeneration of a Pinus pinaster forest in NW Spain. Plant Ecol 197: 81-90

Cottrell TR (2004) Seed rain traps for forest lands:Considerations for trap constructionand study design. BC JEcosystManag - Extension Note 5

Denham AJ, Whelan RJ, Auld TD (2009) Characterizing the Litter in Postfire Environments: Implications for Seedling Recruitment. Int J Plant Sci 170: 53-60

De las Heras J, Martínez-Sánchez JJ, González-Ochoa AI, Ferrandis P, Herranz JM (2002) Establishment of Pinus halepensis Mill. sapling following fire: effects of competition with shrub species. Acta Oecol 23: 91–97

Eshel A, Henig-Sever N, Ne'eman G (2000) Spatial variation of seedling distribution in an east Mediterranean pine woodland at the beginning of post-fire succession. Plant Ecol 148: 175-182

Fernandez C, Vega JA, Jimenez E, Fonturbel T (2011) Effectiveness of three post-fire treatments at reducing soil erosion in Galicia (NW Spain). Int J Wildland Fire 20: 104-114

Ferreira AdB (Ed) (1978) Planaltos e montanhas do norte da Beira – estudo de geomorfologia. Centro de Estudos Geográficos, Lisbon

Fonturbel MT, Vega JA, Perez-Gorostiaga P, Fernandez C, Alonso M, Cuinas P, Jimenez E (2011) Effects of soil burn severity on germination and initial establishment of maritime pine seedlings, under greenhouse conditions, in two contrasting experimentally burned soils. Int J Wildland Fire 20: 209-222

García-Fayos P, Gulias J, Martínez J, Marzo A, Melero JP, Traveset A, Veintimilla P, Verdú M, Cerdán V, Gasque M, Medrano H (2001) Bases ecológicas para la recolección, almacenamiento y germinación de semillas de especies de uso forestal de la Comunidad Valenciana

GarciaFayos P and Cerda A (1997) Seed losses by surface wash in degraded Mediterranean environments. Catena 29: 73-83

Gil L, Lopez R, Garcia-Mateos A, Gonzalez-Doncel I (2009) Seed provenance and fire-related reproductive traits of Pinus pinaster in central Spain. Int J Wildland Fire 18: 1003-1009

Herranz JM, MartinezSanchez JJ, Marin A, Ferrandis P (1997) Postfire regeneration of Pinus halepensis Miller in a semi-arid area in Albacete province (southeastern Spain). Ecoscience 4: 86-90

Madrigal J, Hernando C, Guijarro M, Vega JA, Fonturbel T, Perez-Gorostiaga P (2010) Smouldering fire-induced changes in a Mediterranean soil (SE Spain): effects on germination, survival and morphological traits of 3-year-old Pinus pinaster Ait. Plant Ecol 208: 279-292

Martínez-Sanchez JJ, Ferrandis P, de Las Heras J, Herranz JM (1999) Effect of burnt wood removal on the natural regeneration of Pinus halepensis after fire in a pine forest in Tus valley (SE Spain). For Ecol Manag 123: 1-10

McDonald JH (2009) Handbook of Biological Statistics. Sparky House Publishing, Baltimore, Maryland

Nathan R, Ne'eman G (2004) Spatiotemporal dynamics of recruitment in Aleppo pine (Pinus halepensis Miller). Plant Ecol 171: 123-137

Ne'eman G, Izhaki I(1998) Stability of pre- and post-fire spatial structure of pine trees in Aleppo pine forest. Ecogr 21: 535-542

Otto R, Garcia-del-Rey E, Munoz PG, Fernandez-Palacios JM (2010) The effect of fire severity on first-year seedling establishment in a Pinus canariensis forest on Tenerife, Canary Islands. Eur J For Res 129: 499-508

Pausas JC, Llovet J, Rodrigo A, Vallejo R (2008) Are wildfires a disaster in the Mediterranean basin? - A review. Int J Wildland Fire 17: 713-723

Pausas JG, Ouadah N, Ferran A, Gimeno T, Vallejo R (2003) Fire severity and seedling establishment in Pinus halepensis woodlands, eastern Iberian Peninsula. Plant Ecol 169: 205-213

Pausas JG, Ribeiro E, Vallejo R (2004) Post-fire regeneration variability of Pinus halepensis in the eastern Iberian Peninsula. For Ecol Manag 203: 251-259

Perez B, Moreno JM (1998) Fire-type and forestry management effects on the early postfire vegetation dynamics of a Pinus pinaster woodland. Plant Ecol 134: 27-41

Reyes O, Casal M(2001) The influence of seed age on germinative response to the effects of fire in Pinus pinaster, Pinus radiata and Eucalyptus globulus. Ann for Sci 58: 439-447

Reyes O and Casal M (2002) Effect of high temperatures on cone opening and on the release and viability of Pinus pinaster and P-radiata seeds in NW Spain. Ann For Sci 59: 327-334

Reyes O and Casal M (2004) Effects of forest fire ash on germination and early growth of four pinus species. Plant Ecol 175: 81-89

Rivas-Martínez S, Díaz TE, Fernández-González F, Izco J, Lousã M, Penas A (2002) Vascular Plant Communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. Itiner Geobotanica 15: 5-432

Santos AS (2010) Efeitos dos fogos florestais na dinâmica do azoto e carbono dos solos, na região centro de Portugal. Unpublished MSc thesis, Agrarian High School (ESAC), Coimbra

Saracino A, Pacella R, Leone V, Borghetti M (1997) Seed dispersal and changing seed characteristics in a Pinus halepensis Mill forest after fire. Plant Ecol 130: 13-19

Silva J, Moreira F, Vaz P, Catry F, Ferreira P (2009) Assessing the relative fire proneness of different forest types in Portugal. Plant Biosyst 143: 597-608

Tapias R, Climent J, Pardos JA, Gil L (2004) Life histories of Mediterranean pines. Plant Ecol 171: 53-68

Thanos CA, Daskalakou EN, Nikolaidou S (1996) Early post-fire regeneration of a Pinus halepensis forest on Mount Parnis, Greece. J Veg Sci 7: 273-280

Thanos CA and Skordilis A (1987) The Effects of Light, Temperature and Osmotic-Stress on the Germination of Pinus-Halepensis and Pinus-Brutia Seeds. Seed Sci Technol 15: 163-174

Torres O, Calvo L, Valbuena L (2006) Influence of high temperatures on seed germination of a special Pinus pinaster stand adapted to frequent fires. Plant Ecol 186: 129-136

Trabaud L, Michels C, Grosman J (1985) Recovery of burnt Pinus halepensis Mill. forests. II. Pine reconstruction after wildfire. For Ecol Manag 13: 167-179

Tutin TG, Heywood VH, Burges DH, Valentine DH, Moore DM, Walters SM, Webb DA (Eds)(1964-1980) Flora Europaeae. Cambridge University Press, Cambridge

Ubeda X, Outeiro LR, Sala M (2006) Vegetation regrowth after a differential intensity forest fire in a Mediterranean environment, northeast Spain. Land Degrad Dev 17: 429-440

Vega JA, Fernandez C, Perez-Gorostiaga P, Fonturbel T (2008) The influence of fire severity, serotiny, and post-fire management on Pinus pinaster Ait. recruitment in three burnt areas in Galicia (NW Spain). For Ecol Manag 256: 1596-1603

Vega JA, Fernandez C, Perez-Gorostiaga P, Fonturbel T (2010) Response of maritime pine (Pinus pinaster Ait.) recruitment to fire severity and post-fire management in a coastal burned area in Galicia (NW Spain). Plant Ecol 206: 297-308

WRB (2007) http://www.fao.org/nr/land/soils/soil/wrb-soil-maps/en/. Accessed November 2011

## Supplementary Material

**Supplementary Material 1 -** Average and standard deviation of the cover (in %) of the understory plant species at the nine High and nine Low Crown Consumption plots.

| | | | 18 months post-fire | | | | 36 months post-fire | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | High Crown C. | | Low Crown C. | | High Crown C. | | Low Crown C. | |
| | | | cover (%) | | | | | | | |
| | | | mean | sd | mean | sd | mean | sd | mean | sd |
| Resprouting | ERICACEA | *Arbutus unedo* L. | 3 | 2 | 3 | 3 | 6 | 4 | 8 | 8 |
| | ERICACEA | *Erica australis* L. | 2 | 3 | 1 | 1 | 7 | 7 | 4 | 4 |
| | FABACEAE | *Pterospartum tridentatum* (L.) Willk | 1 | 1 | 2 | 3 | 4 | 4 | 7 | 9 |
| | FAGACEAE | *Quercus suber* L. | 0 | 1 | - | | 1 | 1 | - | |
| | HYPOLEPID. | *Pteridium aquilinum* L. (Kuhn) | - | | 1 | 2 | 4 | 9 | 4 | 6 |
| | LILIACEAE | *Scilla monophyllos* Link. | 0 | 0 | 0 | 0 | - | | - | |
| | LILIACEAE | *Simethis mattiazzi* (Vandelli) Sacc. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | OLEACEAE | *Phyllirea angustifolia* L. | 0 | 1 | - | | 1 | 2 | - | |
| | POACEAE | *Agrostis curtisii* Kérguelen | - | | 1 | 4 | 0 | 1 | 6 | 9 |
| Germinating | CISTACEAE | *Cistus psilosepalus* Sweet | 1 | 1 | 0 | 0 | 3 | 3 | 1 | 2 |
| | CISTACEAE | *Halimium halimifolium* (L.) Willk | 2 | 2 | 0 | 0 | 3 | 2 | 3 | 4 |
| | ERICACEA | *Calluna vulgaris* L. | 1 | 0 | 1 | 2 | 7 | 4 | 9 | 4 |
| | ERICACEA | *Erica cinerea* L. | - | | - | | 1 | 2 | 1 | 2 |
| | ERICACEA | *Erica umbellata* L. | - | | - | | - | | 0 | 1 |
| | SALICACEAE | *Salix* sp. | - | | 0 | 0 | 0 | 0 | 1 | 1 |
| | | anual and bienal herbs | 3 | 3 | 2 | 1 | 2 | 2 | 1 | 1 |

**Chapter 3**

# Wildfire effects on the soil seed bank of a maritime pine stand — The importance of fire severity

## Chapter 3

## Wildfire effects on the soil seed bank of a maritime pine stand — The importance of fire severity

This chapter is published as:

P. Maia, J.G. Pausas, V. Arcenegui, C. Guerrero, A. Pérez-Bejarano, J. Mataix-Solera, M.E.T. Varela, I. Fernandes, E.T. Pedrosa, J.J. Keizer. Wildfire effects on the soil seed bank of a maritime pine stand — the importance of fire severity. 2012. Geoderma. 191: 80-88

### Abstract

This study addressed the impacts of wildfire and, in particular, its severity on the seed bank of the litter/ash layer and the topsoil of a Mediterranean pine plantation (Pinus pinaster Ait.) in north-central Portugal. The study location was selected for presenting a homogeneous pine cover before the fire, on the one hand, and, on the other, heterogeneous patches with distinct degrees of damage to the pine crowns immediately after the fire. The experimental design involved the selection, from the opposite valley side, of three zones with adjacent strips of Low and High Canopy Consumption (L/HCC). Within each of these strips, a transect was laid out along which three plots were established at 10 m intervals. The same was done in the unburnt area immediately outside the fire perimeter. At each plot, samples were collected within the first two weeks after the fire to: (i) asses viable seed densities for three sampling layers, using the indirect method for a 10-month period; (ii) estimate maximum temperature reached (MTRs) at 0–3 cm depth, on the basis of Near Infrared Spectroscopy (NIR). Fire severity at the plots was further determined by verifying, in situ, pine canopy consumption (FCC) as well as by measuring the minimum diameter of remaining shrub twigs (TDI). In comparison with the unburnt area, the recently burnt

area as a whole revealed a substantial increase in overall densities of viable seeds. Seed bank composition, however, varied markedly within the burnt area but this could be explained reasonably well by differential effects of the wildfire associated with its severity, in terms of the two crown consumption classes as well as the TDI index but not the MTRs. The inclusion of the litter/ash layer and the separation of two soil depths were amply justified by providing clear support for the important role of fire severity, in particular for the two principal taxa (*Calluna vulgaris* and *Erica* spp., presumably mainly *E. australis*).

Keywords: Wildfire, Soil seed bank, *Pinus pinaster* Ait., *Erica* spp., *Calluna vulgaris*

### 3.1. Introduction

Fire is a key ecological and evolutionary factor in Mediterranean-type ecosystems (Pausas and Keeley, 2009), therefore many Mediterranean plant species present adaptive traits in relation to fire occurrence (Pausas et al., 2004) like the ability to resprout or to germinate after fire. Post-fire germination can be explained by heat toleration or fire related stimulation (Paula and Pausas, 2008), as well as chemical triggers related to smoke and/or ash exposition (Moreira et al., 2010). However, the role of heating regime in germination depends on the species, as high severity or the exposure to high temperatures may be lethal to the seeds of some species (Moreira et al., 2010; Trabaud, 1992). Besides laboratory experiments (e.g. Moreira et al., 2010; Rivas et al., 2006), also experimental fires, in particular through the use of thermo-couples installed in the topsoil prior to the burning (e.g. Fernandéz et al., 2008; Madrigal et al., 2010), can allow detailed insight in heating effects on germination. Wildfires, on the other hand, typically do not. Instead, the severity of wildfires is commonly evaluated using indices that reflect fire-induced damage to the above-ground vegetation/biomass, such as crown and litter consumption, diameter of

remaining twigs, and colour of ash layer (Keeley, 2009; Otto et al. 2010; Pausas et al., 2003; Pereira et al., 2010; Pérez and Moreno, 1998; Roy et al., 2010; Úbeda et al., 2006). Recent studies, however, have found that Near Infrared (NIR) spectroscopy can give precise estimates of the maximum temperature produced in soils by heating, namely under laboratory conditions (e.g. Arcenegui et al., 2008; Guerrero et al., 2007). To the best of our knowledge, the present study is a first attempt to employ this methodology in a wildfire context, to estimate the temperatures reached in the top soil.

Although Mediterranean pine woodlands are particularly prone to wildfire occurrence (Fernandes and Rigolot, 2007), not all aspects of their post-fire regeneration have received much research attention. Amongst the existing studies, Arianoutsou and Ne'eman (2000), Otto et al. (2010) and Pausas et al. (2003) were limited to the regeneration of the pine populations themselves. Three other prior studies (Calvo et al., 2003; Ferrandis et al., 1996; Valbuena and Trabaud, 2001) did, in fact, assess post-fire recovery of all vascular plants and the role therein of the soil seed bank. However, unlike the present study, these studies, did not explicitly address the impact of fire severity on seedling emergence.

The role of litter layer as a potential source of seeds is not consensual. Litter can have negative (Rebollo et al., 2001) as well as positive effects on germination, due to protection of the seeds from predators, (Denham et al., 2009) or enhanced seed longevity (Rotundo and Aguiar, 2005). Even if the conditions in the litter itself are not favourable for germination or long-term storage, the litter can act as a temporary storage from where the seeds can be incorporated in the soil seed bank by the soil fauna such as earthworms (Zaller and Saxler, 2007). Moreover, the distribution of seeds along the vertical profile of the soil is not homogeneous (Bekker et al. 1998), neither is fire effect, due to the heat-minimizing nature of soil (De Bano et al., 1977 *in* Ferrandis et al. 1996). Therefore, this study considered the vertical distribution of seeds in the top soil, including litter as a potential source of viable seeds, before and after the fire.

The principal aim of this study is to further the knowledge of direct effects of wildfire on the soil seed bank of Mediterranean pine woodlands. The study's specific objectives are the following: (1) to evaluate the wildfire effect on the soil seed bank, in terms of seed density and species composition, (2) to assess in which extent these effects are related to fire type, as defined by the proportion of crown consumption or (3) to more detailed measures of fire severity. The latter included (3.1) an index based on the traditional measurement of the diameters of the burnt twigs and also (2.2) the estimation of maximum temperature reached (MTR) on the soil using near infrared spectroscopy (NIR). By doing so, we also provided an evaluation of the different fire severity estimations.

## 3.2. Materials and methods

### 3.2.1. Study Area

The study area is located near the village of Colmeal, in north-central Portugal (**Figure 3**). It was burnt by a wildfire that occurred on August 24 2008, destroying in total some 70 ha of mainly MaritimePine (*Pinuspinaster* Ait.) and eucalypt (*Eucalyptus globulus*Labill.) plantations.

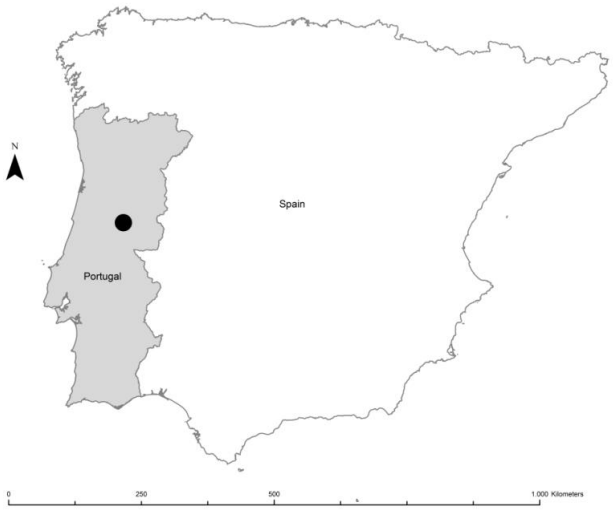



**Figure 3** –Location of the study are (black circle) in the Iberian Peninsula.

Within the study area, a west-facing slope covered with Maritime pine (40º08'45.77''N, 7º59'08.22''W, elevation between 468 and 525 m a.s.l.) was selected for this study The main reasons for selecting this particular slope were (i) it constituted a rather homogeneous stand prior to the fire, as was evident from existing images available at Google Earth and was in line with the fact that it pertains to the common lands of the Arganil municipality and, as such, is being managed by the AFN, the Portuguese National Forestry Authority);(ii) the slope was only partially burnt by the 2008 wildfire, on the one hand, and, on the other, revealed clear signs of contrasting fire severities within the burnt area, namely well-defined differences in the consumption of the pine crowns that could easily be recognized from the opposite side of the valley (see also section 3.2.2) According to information provided by various tree ring counts carried out following the felling of the burnt area, the pine stand was estimated to be approximately 25 years old at the time of the wildfire. . The pine tree density before the fire was around 2700 trees $ha^{-1}$. The understory vegetation at the unburnt part of the slope was mainly composed of the shrubs *Arbutus unedo*L., *Erica australis*L., *Calluna vulgaris* (I.) Hull,*Pterospartum tridentatum (*L.) Willk and *Phyllirea angustifolia*L. and the grasses *Agrostis curtisii* Kerguélen and *Agrostis delicatula* Pourr.ex Lapeyr (nomenclature is according to Tutin et al. (1964-1980)).

The climate of the study area can be classified as Meso-Mediterranean (Rivas-Martínez et al., 2002). The mean annual temperature is estimated to be between 10 and 12.5 $^{o}$C, and the average annual rainfall between 1400 and 1600 mm (APA, 2011: 1931 - 1960). Two soil profiles suggested that the soils at the study site are predominantly Leptosols (WRB, 2006), and that the topsoil (0-5 cm) has a sandy loam to loam texture (sand: 29-54 %; silt: 29%; clay: 16-22 %) (Santos, 2010). The underlying rocks are pre-Ordovician schists of the Hercynian Massif (Ferreira, 1978).

### 3.2.2. Experimental design

Visual observation and photographs taken from the opposite side of the valley resulted in the selection of three zones where fire severity as indicated by degree of pine crown consumption had varied markedly over short distances. Dark-coloured areas were taken to reflect the (almost) complete consumption of the pine crowns, whereas light-coloured areas were interpreted to correspond to scorched crowns retaining substantial amounts of - dead - needles. The identification of adjacent areas of high and low crown consumption was done for the purpose of implementing an experimental design involving paired observations of contrasting fire severities. However, *in-situ* estimation of pine crown consumption (see underneath) obliged to a re-classification of one of the dark-coloured as well as one of the light-coloured areas, such that the experimental design continued balanced but did no longer involve paired observations.

A total of six transects with a length of approximately 30 m were laid out in the three pairs of adjacent burnt areas of apparent high and low crown consumption. An additional transect was located in the unburnt slope part nearby the fire perimeter. All transects were laid out in a perpendicular direction to the contour lines and on basically the same slope positions, so as to minimize differences in topographic and soil conditions. Along each transect, three plots of 25 $m^2$ were established at intervals of roughly 10 m, thus giving a total of 21 plots.. In each plot, the number of totally and partially combusted crowns was counted, and the percentage of fully combusted crowns (FCC) was calculated for each plot. Based on the plot-wise FCC values, the transects in the burnt areas were classified as Low Crown Consumption (LCC) or High Crown Consumption (HCC), with FCC values ranging from 0 to 13(mode 0) and 17 to 50 (mode 50), respectively. As mentioned above, this involved a re-classification of two transects compared to the original classification from a distance.

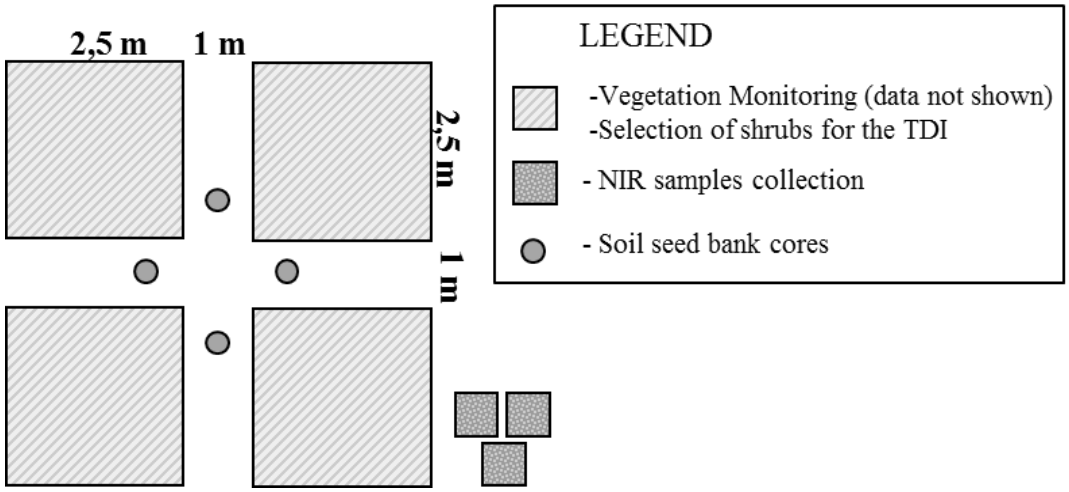



**Figure 4** – Layout of the vegetation plots and of the sampling points of the seed bank cores (see section 2.3) and the NIR samples (see section 2.5) .

### 3.2.3. Soil seed bank sampling and assessment

The soil seed bank was sampled approximately two weeks after the wildfire, before the occurrence of any rain. In the center of each plot (**Figure 4**), four cores with a diameter of 6 cm were inserted into the soil to a depth of roughly 10 cm, carefully removed and transported to the laboratory, and then separated in three sub-samples: (i) ash[1]or litter (in the case of the burnt and unburnt plots, respectively); (ii) 0-3 cm soil depth and (iii) 3-6 cm soil depth. Then, the soil was sieved with a mesh of 2 mm, and the coarser particles were thoroughly inspected for pine seeds in particular.

All 252 resulting sub-samples were placed separately in aluminum trays, which had been previously perforated, on top of a 3 cm thick layer of vegetable substrate and vermiculite (1:1), and then put to germinate in a greenhouse under natural photo-period and ambient temperature conditions. The trays were regularly watered with distilled water and inspected for seedling emergence during a period of 9 months (November2009-July2010) and 1 additional months with no germination observed, to assure all viable seeds had emerged. 60% of the seedlings could be identified at the species level, whilst from the remaining seedlings only five could not be identified at the genus level but only at the family level as pertaining to the Asteraceae and Poaceae.

### 3.2.4. Twig Diameter Index (TDI)

Within each plot, up to 10 burnt shrubs were randomly selected, and the diameters of their 3 thinnest remaining twigs were measured. The average diameter was calculated for each plot and then re-scaled by dividing by the maximum diameter measured in this study. The resulting index, called Twig Diameter Index (TDI) ranged from 0 to 1 i.e. from low to high twig consumption and, thus, fire severity.

### 3.2.5. NIR-based estimation of the maximum temperature reached in soils

#### 3.2.5.1. Model relating NIR spectra with MTR

At various points along the unburnt transect, a large (about 20 kg), composite soil sample was collected at 0-3 cm depth, carefully excluding the litter and duff layer. This soil sample was air-dried, sieved with a 2 mm mesh, and then stored in paper bags. At a later stage, a wide range of controlled heating treatments, combining different heating temperatures and durations, were carried out with aliquots of 30 g of the unburnt soil but subjecting each aliquot to a separate and single treatment. This was done in an muffle furnace, using thermo-couples (k-type, NiCr-Ni; Testo SA, Barcelona, Spain) to measure the MTR reached at 2 cm depth inside the sample.

After cooling the aliquots to room temperature and placing them in glass Petri dishes, their NIR-spectra were measured using a FT-NIR spectro-photometer (MPA; BrukerOptik GmbH, Germany), that was equipped with a quartz beam splitter, a PbS-detector as well as an integrating macro-sample sphere and a rotating sample cup to allow for scanning large areas of the samples. The scanning was done in reflectance mode from 12000 to 3800 $cm^{-1}$, which is approximately equivalent to a range of 830 to 2630 nm.

To reduce optical interference not related to the chemical composition of the sample, such as, for example, those variations caused by different sample particle size (Blanco and Villarroya, 2002), typical procedures of pre-processing the spectra were tested.

They included no pre-processing, first derivative, second derivative, linear offset subtraction, straight line subtraction, multiplicative scatter correction, vector normalization, min-max normalization, and combinations thereof. Derivative treatment is considered to reduce scattering effects as well to enhance the resolution of the spectral peaks (Burns and Ciurczak, 2001). Several combinations were tested using OPUS 5.5 (BrukerOptik GmbH, Ettlingen, Germany) during calibration. First derivative and vector normalization was the combination that produced the lowest root mean squared error of cross-validation (RMSECV), therefore being selected for the present work.

Partial least squares (PLS) regression was used to construct the model (i.e. the empirical calibration function) relating the NIR-spectra with the MTR of the unburnt soil during the various heating experiments (McCarty et al., 2002; Viscarra Rossel et al., 2006). In this study, the leave-one-out cross-validation method was used. The resulting model, which provided the most satisfactory fit between the measured MTR and the MTR predictions based on the NIR-spectra was used to estimate the MTR in the burnt soils (**Figure 5**).

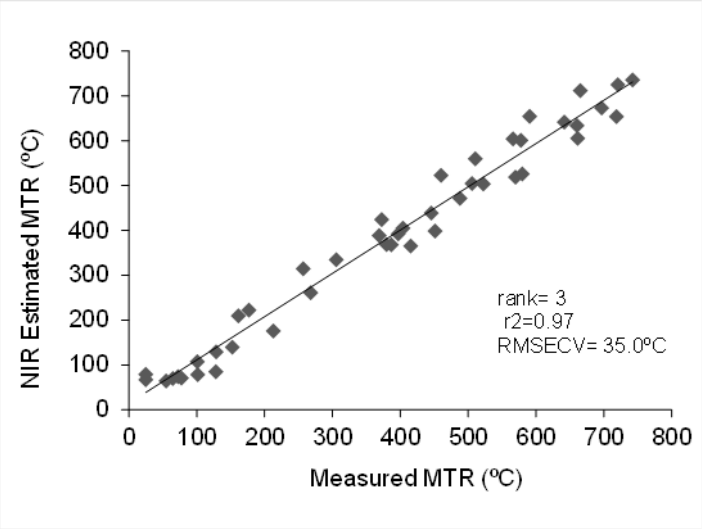



**Figure 5** - Relationship of the maximum temperatures reached (MTR) in unburnt soils as measured in laboratory heating experiments with the MTR predicted on the basis of the corresponding near-infrared (NIR) spectra.

#### 3.2.5.2. Estimation of MTR of the burnt soils

At each burnt plot, a sample of the top 3 cm of the soil was collected at three nearby sampling points according to the scheme in Figure 2. Ashes were gently but thoroughly removed from the soil surface prior to sampling, to avoid any interference with the NIR-spectra (Arcenegui *et al.* 2008). Sample handling and subsequent analysis with the FT-NIR spectrophotometer was basically the same as described above for the unburnt soil, except that the aliquots comprised 50 g of soil.

Each of the diffuse reflectance measurements involved 64 scans, which results were averaged. Furthermore, each sample was measured twice, thereby increasing the surface of soil sample scanned, and these results were also averaged. The resolution used for spectral analysis was 8 $cm^{-1}$. Background corrections were made before each sample scan. The time used for the spectral measurement was approximately 1 min per sample. No chemical or hazardous reagents were needed to obtain the NIR spectra.

The NIR-spectra were then used to estimate the MTR of the burnt samples, applying the model that was constructed earlier (see section 3.2.5.1).

### 3.2.6. Data analysis

Statistical data analysis was carried out with IBM SPSS Statistics 19. Preference was given to non-parametric statistical tests, because of the limited number of samples and the resulting difficulties in verifying key assumptions underlying the parametric equivalents. Therefore, differences between the two fire severity classes of Low and High Crown Consumption (LCC vs. HCC) were tested for their significance using the Mann-Whitney *U* test.

## 3.3. Results

### 3.3.1. Relation of crown consumption classes with other fire severity indices

The results from the near-infrared spectroscopy (NIR) indicated that the upper, 0-3 cm soil layer suffered low to moderate heating by the wildfire, according to the criteria of Wohlgemuth et al. (2006). The maximum temperatures reached (MTRs) varied markedly between the 18 burnt plots, ranging from 53 to 125$^{o}$C.The median MTR of the LCC plots (86$^{o}$C) was slightly higher than that of the HCC plots (78ºC) but the MTRs of the two crown consumption classes were not significantly different (Mann Whitney *U*-test: p =0.31), as is also easily understood from **Figure 6**a.

The diameters of the burnt twigs also indicated considerable variation in fire severity amongst the 18 burnt plots, with the minimum and maximum TDI values differing an order of magnitude (0.05 – 0.51). Unlike in the case of the MTRs, the TDI values of the LCC plots were significantly lower and, thus, consistent with a lower severity,than those of the HCC plots (Mann Whitney *U*-test: p =0.005) (**Figure 6**).

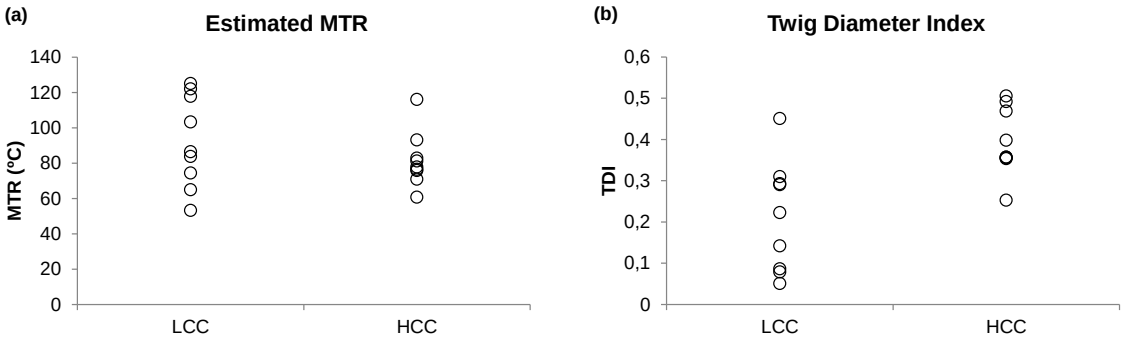



**Figure 6** - Maximum temperatures reached (MTRs: a) and twig diameter index values (TDI: b) for the individual plots with Low vs. High Crown Consumption (L/ HCC)s.

### 3.3.2. Seed bank composition

The overall density of viable seeds in the litter layer and the top 6 cm of the unburnt soil amounted to 1003 seeds $m^{-2}$, whereas the overall density in the ash layer and burnt soil (LCC and HCC plots) was roughly 50% higher (1445 seeds $m^{-2}$;

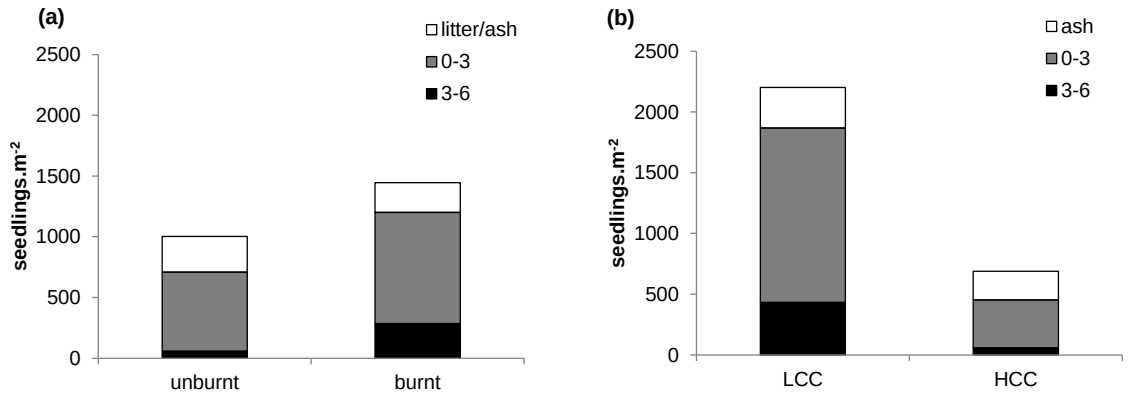
**Figure** 7a) This difference was mainly due to the upper soil layer (0-3 cm: 649 *vs.* 914 seeds $m^{-2}$). Somewhat surprisingly, the overall densities were basically the same for the litter and ash layer (295 and 285 seeds $m^{-2}$, respectively).

The overall effect of fire on germination differed markedly between LCC and HCC plots (

**Figure** 7b).The overall seed density of the nine LCC plots (2203 seeds $m^{-2}$) was more than twice that of the unburnt plots, especially due to the two soil layers 0-3 (+120%) and the 3-6 cm (+630%). The nine HCC plots, on the other hand, revealed a negative effect of fire, as the overall density was about 30% lower than the unburnt plotsThis reduction on viable seed density was largely due to the upper soil layer ( 0-3 cm: -40%). As a result of these opposite tendencies, the LCC samples contained approximately four times more viable seeds than the HCC samples. Whilst LCC densities were consistently higher than HCC densities for all three sample layers, the relative differences increased along the soil profile (ash layer: +40 %;.0-3 cm: +265%; 3-6 cm: +630%).

The floristic composition of the viable seed bank consisted of 10 taxa pertaining to eight higher plant families. Seven of these families - Compositae (Compositae sp1) Caryophyllaceae (*Spergula pentandra*L.), Cistaceae (*Halimium* sp1), Fabaceae (*Pterospartum tridentatum*(L.)Willk), Pinaceae( *Pinus pinaster*Ait.) Poaceae (*Agrostis curtisii* Kerguélen and *Agrostis delicatula* Pourr. ex Lapeyr, Poacaea sp1), and Scrophulariaceae (*Anarrhinum bellidifolium*L.) - occurred at very low frequencies, amounting to just 13 % of the total number of viable seeds, and were therefore analysed together ("other spp."). The predominant family was the Ericaceae, with

seeds of *Calluna vulgaris* (I.) Hull*, Erica umbellata* Loefl.ex L. and *E. australis*L. Due to premature death of many seedlings it was impossible to distinguish between the two *Erica* spp. for the bulk of the samples. Although *Erica* spp. was analysed here as a single taxon, *E. australis* was held to be the principal species. This opinion was based on the species' predominance in the understory of the unburnt part of the pine plantation as well as its predominance amongst the *Erica* spp. seedlings that have emerged after the wildfire and were recorded in the vegetation monitoring plots as shown in **Figure 10**.The most striking difference in overall floristic seed bank composition between the unburnt and burnt (LCC and HCC) samples wasthe total absence of *Calluna vulgaris* in the former vs. its elevated abundance in the latter, amounting to 39 % of the overall seed density (560 seeds $m^{-2}$; Figure 5a). All three sample layers contributed appreciably (>100 seeds $m^{-2}$) to the overall abundance of *C. vulgaris*, even turning it into the dominant *taxon* of the ash layer (80 %). The higher overall density of *Erica* spp. in the burnt than unburnt samples (698 vs. 472 seeds $m^{-2}$) reflected a more complex pattern. Namely, the ash layer contained less viable Erica spp. seeds than the litter layer (-75 %), whilst the opposite was true for the two soil layers(0-3 cm - +50%; 3-6 cm138 vs. 0 seeds.$m^{-2}$). The lower "other spp." on the other hand, revealed consistently lower densities in the burnt than unburnt samples for all




three sample layers (-89%(ash/litter), -53 % (0-3cm soil) and –50 % (3-6cm soil)) .

**Figure 7** - Overall seed densities in the three sample layers (litter/ash, and 0-3 and 3-6 cm soil depth) for the unburnt vs. burnt plots (a) and for the plots with Low vs. High Crown Consumption ( L/HCC:b).

The above-mentioned fire-induced germination of *Calluna vulgaris* was evidenced by both LCC and HCC plots (b). In the case of the LCC plots, this inducement was clearly less pronounced for the lower soil depth (79 seeds.m$^{-2}$) than for the ash and upper soil layer (374 and 0 472 seeds.m$^{-2}$, respectively).

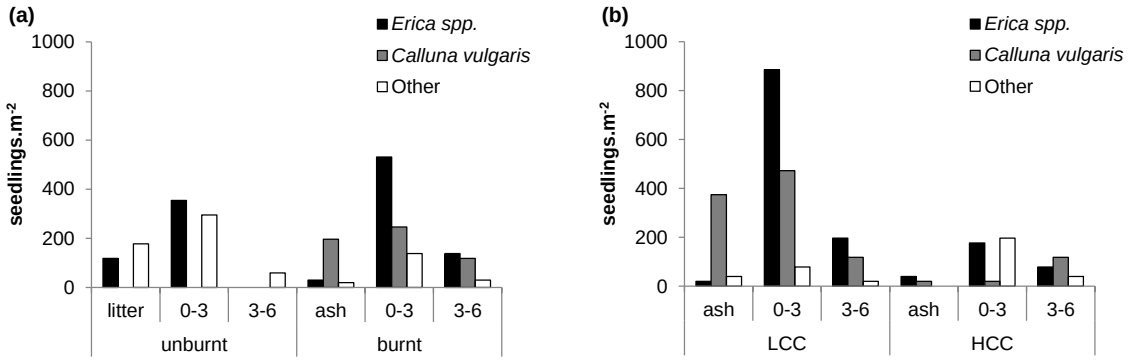



**Figure 8** –Seed densities of the individual taxa in the three sample layers (litter/ash, and 0-3 and 3-6 cm soil depth) for the unburnt vs. d burnt plots (a) and for the plots with Low vs. High Crown Consumption ( L/ HCC: b).

In the case of the HCC plots, by contrast, the *Calluna vulgaris* seed density was marked higher in the lower soil layer (188 seeds.m$^{-2}$) than in the other two sample layers (ash: 20 seeds.m$^{-2}$; 0-3 cm: 20 seeds.m$^{-2}$). Thus, this contrast between the HCC and LCC results mainly reflected relatively low densities in the ash and upper soil layers of the HCC compared to the LCC plots.

The seed densities of *Erica spp*. suggested opposite fire effects for the two crown consumption classes in the case of the upper soil layer but not in that of the other two sample layers. Namely, the ash layer of both the LCC and HCC plots contained notably less viable *Erica spp*. seeds than the litter layer of the unburnt plots (-83 and 67%, respectively)and the lower soil layer of both the LCC and HCC plots contained viable seeds contrary to that of the unburnt plots (197 and 97 seeds m$^{-2}$, respectively). The

upper soil layer, on the other hand, revealed a marked increase in Erica spp. germination for the LCC plots (+106 %) as opposed to a clear decrease for the HCC plots (-83 and 63%, respectively).The "other spp." revealed a straightforward fire effect, with both LCC and HCC plots. Even so, this reduction in viable seed densities was consistently bigger for the HCC that LCC plots. (ash layer:-100 vs. -77 %; 0-3 cm: -73 vs. –33 %; 3-6 cm:- 66 vs. –33%).

### 3.3.3. Seed bank spatial patterns and relation with fire severity indices

The higher overall seed density of the LCC than HCC plots was evident at the scale of the transects (**Figure 10**a). The overall densities of the LCC transects varied between 1652 and 2596 seeds $m^{-2}$, whereas those of the HCC transects were consistently below 1000 seeds.$m^{-2}$ (354 to 944 seeds.$m^{-2}$). From the three sampling layers, however, only the upper soil layer contributed consistently to the higher densities of the LCC than HCC transects. Consistently higher densities for the LCC than HCC transects were also revealed by the two principal *taxa* (**Figure 10**b, c). Spatial variability was especially pronounced in the case of the LCC transects. This was due to one particular transect but a different one in the case of *Erica spp.* than of *C. vulgaris*. The individual sampling layers did not tend to play a straightforward role in the consistent transect-wise differences of the two predominant *taxa*. An exception was the upper soil layer for *Calluna vulgaris*. At the transect scale, the marked spatial variability in various key seed bank components within the burnt area could be well explained well by the twig-base severity index. This was especially the case when analyzing the seed densities of the three sample layers together. The total seed densities of the two principal *taxa* as well as of all *taxa* together (**Figure 11**a) were closely associated with the transects' average TDI values, with the amounts of viable seeds decreasing with increasing TDI values and, thus, increasing fire severity. The respective Spearman's rank correlation coefficients --0.81 and -0.89 for Erica spp. ($p = 0.05$); and *Calluna*

*vulgaris* (p = 0.02), and even -0.94 for all *taxa* (p =0.005). These significant relationships were to an important extent due to the upper soil layer, as the Spearman coefficients for this layer separately were also relatively high (-0.71 to -0.78), even though non-significant (p = 0.07-0.12).

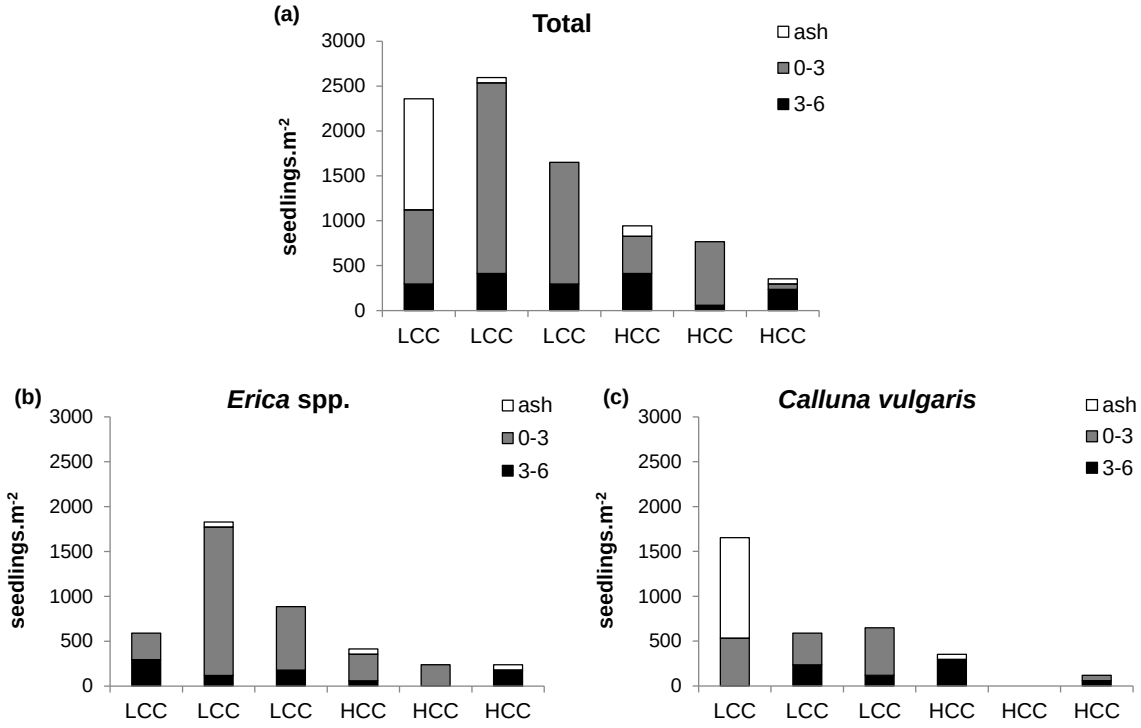



Figure 9 – Seed densities of all *taxa* together (a), *Erica* spp. (b) and *Calluna vulgaris* (c) densities in the three sample layers (ash; 0-3 and 3-6 cm soil depth) for the six transects, classified according to Low vs. High Crown Consumption and ordered according to increasingvalues of the Twig Diameter Index (TDI).

By contrast, transect-wise seed densities were poorly related to the NIR-based severity index. No significant monotonic relationships were found for either the seed densities of the three sampling layers together or the densities of the upper soil layer, for which the best association was expected as the MTRs concerned the same sampling depth (**Figure 11**b). The Spearman correlation coefficients for *C. vulgaris*

were remarkable in suggesting a tendency for an increase in viable seed density with increasing MTR and, thus, increasing fire severity, most markedly so in the case of the 0-3 cm soil layer (ρ= 0.62; p = 0.019).

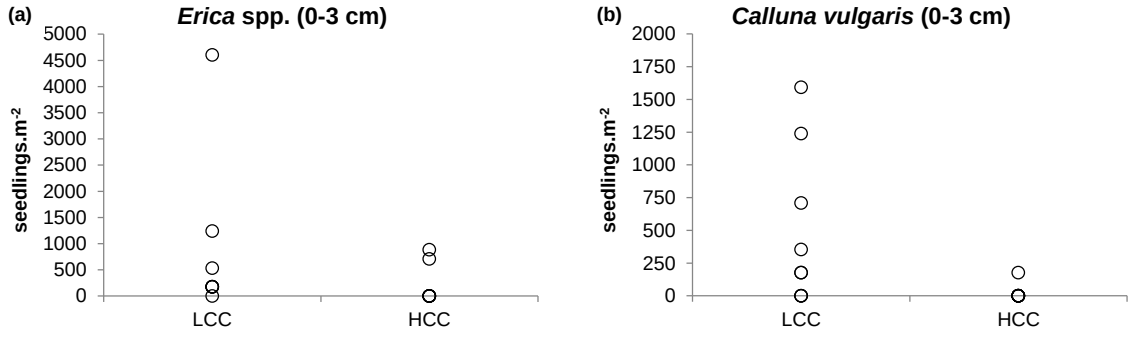



**Figure 10** – Seed densities of *Erica* spp. (a) and *Calluna vulgaris* (b) in the upper soil layer (0-3 cm) for the individual plots with Low vs. High Crown Consumption (L/ HCC).

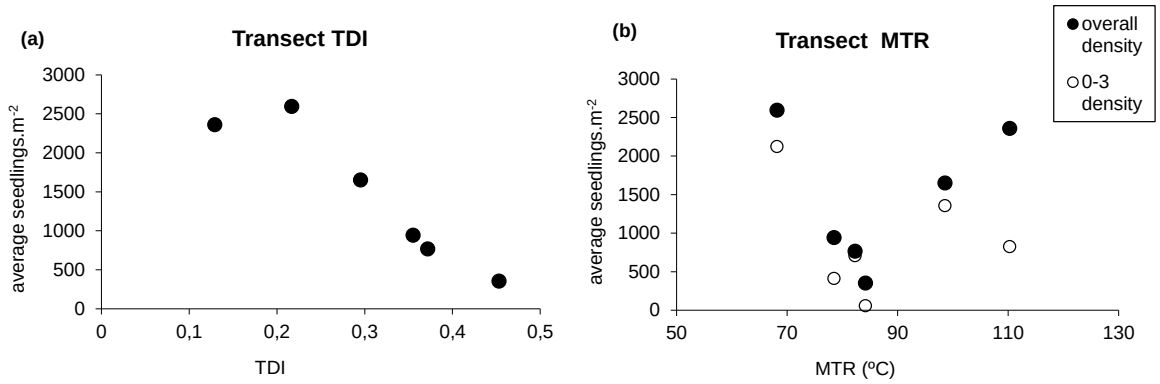



**Figure 11** - Relation of the seed densities of the six transects (overall: all sampling layers) with their average values of the Twig Diameter Index (TDI: a) and Maximum Temperature Reached (MTRs: b).

The germination results at the plot scale provided statistical evidence in support of the earlier notions that overall and transect-wise seed densities decreased with fire severity as indicated by the two crown consumption classes. Namely, the two principal *taxa*

both revealed significantly more viable seeds in the upper soil layer of the LCC plots than of the HCC plots

(Mann Whitney *U*-test: *Erica spp.*, p = 0.023; *C. vulgaris*, p = 0.014), notwithstanding the marked spatial variability amongst the LCC plots in particular (Figure 8). The same tendency was suggested for the total seed densities of *Erica spp.* and *Calluna vulgaris*, with Mann Whitney *U*-test results at the border of significance (p = 0.66 and 0.63, respectively). Seed densities of all *taxa* together likewise hinted towards real differences between the LCC and HCC plots, especially for the upper soil layer (Mann Whitney *U*-test: p = 0.089).

Unlike at the transect scale, at the plot scale the TDI values offered little explanation for the variability in seed densities within and between the two crown consumption classes. The Spearman's rank correlation coefficients for the various combinations of *taxa* and sampling layers were below 0.40 (p > 0.15), with two exceptions. From these exceptions, the *C. vulgaris* densities in the upper soil layer were significantly related with the TDI values (ρ= -0.47, p = 0.045), whilst the total densities in the ash layer were almost (ρ= -0.46, p = 0.056).

The above-mentioned, poor relation of MTRs with seed densities at the transect scale extended to the individual plots. Without exception, Spearman correlation coefficients did not differ significantly from zero, either for the seed densities of the three sampling layers together (ρ= -0.32 to -0.15; p > 0.20) or for the densities of the 0-3 cm soil depth (ρ= -0.31 to -0.08; p > 0.20).

### 3.4. Discussion

The observed difference in overall viable seed density within and outside the burnt area contrasted sharply with the findings from the prior studies that quantified pre- and post-fire seed banks of Mediterranean pine stands in a comparable manner, in particular by including all vascular plants and by employing the indirect assessment method

(Ferrandis et al., 1996; Valbuena et al., 2000a). Whilst the present results indicated a marked enhancement in viable seed numbers (+50 %), the results of of Ferrandis et al. (1996) and Valbuena et al. (2000a) suggested substantial decreases of 25 % and more. An explanation for these opposing effects was suggested by the present results. Namely, seed densities differed noticeably between the two fire severity classes as distinguished on the basis of the degree of consumption of the pine canopies by the flames, with the higher severity class revealing lower densities in terms of overall, transect-wise as well as (in a statistically significant manner) plot-wise figures. Ferrandis et al. (1996) explicitly referred to their wildfire as intense, due to the prevailing weather conditions. More importantly perhaps, their seed bank data were also consistent with a higher fire severity than in the present study. The authors found significantly less viable seeds in their upper than lower soil layer (0-2 vs. 2-5 cm depth; using the indirect method) and, at the same time, a large number of burnt seeds in the upper layer as opposed to none in the lower layer (using the direct method). The present results, on the other hand, revealed higher viable seed densities in the upper than lower soil layers - not only for the unburnt area but also for both crown consumption classes - and, furthermore, MTRs for the upper soil layer that were generally below 100-110 $^{o}$C, i.e. temperatures that have been found to enhance the germination of at least the two Erica species *(E. ausralis*: Cruz et al., 2003; *E. umbellata:* Gonzalez-Rabanal and Casal, 1995).

Besides fire severity, other factors could contribute to the discrepancies between the present results and those of Ferrandis et al. (1996) and Valbuena et al. (2000a). Ferrandis et al. (1996) studied the same pine species as here but the floristic composition of the seed bank was very distinct, being dominated by Cistaceae (*Cistus monspeliensis* and *C. albidus*), Fabaceae (*Trifolium glomeratum* and *T. campestre*) and *Rosmarinus officinalis*, and, thus, reflecting a distinctive phytosociological and biogeographical vegetation unit. This floristic difference could also be the reason for the comparatively high post-fire viable seed density in Ferrandis et al. (1996: 2200

seeds.m2), especially if their fire severity was indeed considerably higher than in the present study as argued before. Valbuena et al. (2000a), on the other hand, concerned a different pine species (*Pinus sylvestris)* but an understory as well as a seed bank that, like here, were dominated by Ericaceae (by *Erica australis* and *Calluna vulgaris*, and by *E. australis*, respectively). Remarkably, Valbuena et al. (2000a) reported exactly the same figure for the viable seed density of the upper 5 cm of the unburnt soil as was found here for the upper 6 cm (i.e. without the litter layer: 708 seeds.$m^{-2}$).

Valbuena et al. (2000a) attributed the observed, negative impact of the wildfire first and foremost to high temperatures-induced damage to *Erica australis* seeds, in agreement with unpublished laboratory germination trials by the same authors as well as by an experimental heathland fire (Valbuena et al., 2000b). Assuming that *Erica australis* was indeed the determinant component of *Erica spp.*, such a temperature-dependent effect would fit in with the present results. Namely, it could explain well: (i) the lower *Erica spp.* viable seed densities in the ash than litter layer as well as in the upper soil layer of the HCC than unburnt plots; and, at the same time, (ii) the higher densities in upper soil layer of the LCC than unburnt plots as well as in the lower soil layer of the burnt than unburnt plots. Perhaps more compelling evidence for contrasting heating effects on the germination of *Erica spp.* was provided by the statistically significant differences between the two crown consumption classes as well as the strong, quantitative relationship with the twig-based fire severity index (TDI). In accordance with Cruz et al. 2003), the threshold for temperature-induced damage to *Erica australis* seeds would lie between 100$^{o}$C (enhancement) and 150$^{o}$C (no germination), at least for short exposure periods (5 min). Possibly, the importance of exposure period could explain the lack of relationships between *Erica spp.* seed densities and the NIR-based estimates of the maximum temperatures reached in the topsoil (MTRs), especially in cases like the present one in which MTRs are relatively low (Wohlgemuth et al., 2006). In addition to fire severity, genetic differences between populations resulting from distinct fire-related adaptive pressures could contribute to the observed discrepancies in the germination

ecology of *Erica australis* (Pausas et al., 2006). *Calluna vulgaris* revealed a less complex response to fire than *Erica spp.* in that its germination was induced by both fire severities. Like in the case of *Erica spp.*, however, there was ample evidence that this effect was markedly stronger for the plots with low than high crown consumption, except at the lower sampling depth. The evidence included statistically significant, inverse relationships of viable seed density with TDI values, not just at the scale of the transects but also at that of the individual plots. The latter was exceptional for this study, due to the pronounced spatial variability in seed bank composition. Valbuena et al. (2000b) also found a noticeable increase in *C. vulgaris* viable seed densities following fire but this concerned an experimental fire of a heathland. Even so, Paula et al. (2009) reported the response of *Calluna vulgaris* to be highly variable, covering the full range of negative to positive effects, with a possible role therein of differences between populations.

The degree of pine crown consumption proved to be a reasonably good indicator of viable seed densities immediately after wildfire. Its principal advantage - i.e. allowing a quick assessment from a distance, including from remotely sensed images - was nonetheless offset to a considerable extent by the need for *in-situ* validation (as explained in section 2.2). The pronounced spatial variability in seed densities within the two crown consumption classes distinguished in this study could be accounted for rather well by the twig-based index (TDI), in particular for contiguous zones such as the transects but not for specific locations such as the sampling plots. Although TDI clearly provided a less subjective and more quantitative measure of fire severity than crown consumption, its time-consuming nature would seem an important limitation for widespread application under practical circumstances. The most laborious of the three fire severity indices applied here (MTR) was poorly related to the other indices as well as to viable seed densities, even at the transect scale. This could perhaps be explained by the limited significance of MTR as single and sole descriptor of heating regime, especially when MTRs are relatively low as was the case here.

### 3.5. Conclusions

The principal conclusions of this study into the direct effects of wildfire and, in particular, its severity on the seed bank of the litter/ash layer and topsoil (0-6 cm) of a Mediterranean pine stand of *Pinus pinaster* in north-central Portugal were the following:

1. Overall densities of viable seeds were substantially higher in the burnt area than immediately next to it but this reflected opposite effects in accordance with fire severity as distinguished based on degree of damage to the pine canopies, i.e. a germination enhancement in the case of the plots with Low Crown Consumption (LCC) *vs.* a decrease in the case of the plots with High Crown Consumption (HCC);

2. The marked variability in viable seed densities between and within the LCC and HCC severity classes could be explained well by the severity index based on the diameters of remaining twigs (TDI), in particular when aggregating the data at the scale of the transects, but not by the maximum temperatures reached in the upper soil layer (0-3 cm) as derived from near infrared spectroscopy (NIR);

3. The densities of viable seeds in the topsoil were similar to those of prior studies in (un)bunrt Mediterranean pine stands but the floristic composition of the seed bank was relatively poor and strongly dominated by Ericaceae, and, as such, compared better to that of *Pinus sylvestris* stand in north Spain than that of a *Pinus pinaster* stand in southeast Spain;

4. The viable seed densities of both predominant *taxa* – *Erica spp.*, presumably by and large *E. australis*, and *Calluna vulgaris* - revealed contrasting tendencies not only with respect to fire severity in terms of LCC/HHC as well as TDIs but also in relation to the different sampling layers, plainly justifying the additional efforts involved.

**Acknowledgements**

The PhD grant of P. Maia has been financed by FCT and QREN, the post-doc grant from M. Varela has been financed by FCT, the Leonardo da Vinci fellowships of I. Fernandes and E. Pedrosa were financed by the European Union. EROSFIRE II project, which gave the logistic sup- port for the field campaigns, was financed by FCT. The Integrated Ac- tion that supported the NIR model development was financed by the Portuguese and Spanish governments. We also thank the AFN and GTF of Arganil, as the responsible for the management of this area, the GTF of Gois for the info on the burnt area, and the Junta de Fregue- sia of Colmeal for their logistic support. A special thanks to all the people who have helped in the installation of the study area, con- struction of the greenhouse and field sampling — Ana Vasques, Carli Mertopawiro, Roel Toonen, Diana Vieira, Robert Broekhuis, Martijn Van den Aker and José Velasco and also to two anonymous reviewers whose comments helped improving this manuscript in a significant way.

**References**

APA: Agência Portuguesa do Ambiente 2011. http://sniamb.apambiente.pt/webatlas/. Last time viewed November 2011.

Arcenegui, V., Guerrero, C., Mataix-Solera, J., Mataix-Beneyto, J., Zornoza, R., Morales, J., Mayoral, A.M., 2008.The presence of ash as an interference factor in the estimation of the maximum temperature reached in burned soils using near-infrared spectro- scopy (NIR). Catena 74, 177–184.

Arianoutsou, M. &Ne'eman, G., 2000. Post-fire regeneration of natural *Pinushalepensis*forests in the East Mediterranean Basin. In: Ne'eman, G. &Trabaud, L. (eds). Ecology, Biogeography and Management of Mediterranean Pine Forest.Backhuys Publishers, 269-290.

Bekker, R.M., Bakker, J.P., Grandin, U., Kalames, R., Milberg, P., Poschold, P., Thomson, K., Willems, J.H., 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. Functional Ecology.12,834-842.

Blanco, M., Villarroya.I., 2002. NIR spectroscopy: A rapid-response analytical tool. Trends Analyt. Chem. 21:240–250.

Burns, D.A., Ciurczak, E.W. (ed.) 2001. Handbook of near-infrared analysis.Second edition, revised and expanded.Marcell Dekker, New York.

Calvo, L., Santalla, S., Marcos, E., Valbuena, L., Tárrega, R., Luis, E., 2003. Regeneration after wildire in communities dominated by *Pinus pinaster*, an obligate seeder, and in others dominated by *Quercuspyrenaica*, typicalresprouter. Forest Ecology and Management 184, 209-223.

Cruz, A., Pérez, B., Velasco, A., Moreno, J. 2003. Variability in seed germination at the interpopulation, intrapopulation and intraindividual levels of the shrub Erica australis in response to fire-related cues. Plant Ecology 169:93-103.

De Bano, L.F., Dunn, P.H., Conrad, C.E., 1977. Fire's effect on physical and chemical prop- erties of chaparral soils. In: Mooney, H.H., Conrad, C.E. (Eds.), Symposium on Envi- ronmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. Forest Service General Technical Report WO-3, Washington, pp. 65–74.

Deham, A., Whelan, R.J., Auld, T., 2009. Characterizing the litter in postfire environments: implications for seedling recruitment. Int. J. Plant Sci. 170(1), 53-60

DíazVizcaíno, E.A., Iglesia Rodríguez, A., Fernández, M., 2006. Interannual variability in fire-induces germination responses of the characteristic Ericacea of the NW Iberian Peninsula. Forest Ecology and Management. 234, S179.

Fernandes, P., Rigolot, E., 2007. The fire ecology of maritime pine (*Pinuspinaster* Ait.). Forest Ecology and Management. 241, 1-13.

Fernández, C., Vega, J.A., Fonturbel, T., Jiménez, E., and Pérez, J.R., 2008. Immediate effects of prescribed burning, chopping and clearing on runoff, infiltration and erosion in a shrubland area in Galicia (NW Spain). Land Degrad. Develop. 19, 502–515.

Ferrandis, P., Herranz, J.M., Martínez-Sánchez, J.J., 1996. The role of seed bank in the early stages of plant recovery after fire in a *Pinuspinaster* forest in SE Spain. Int. J. WildlandFire 6(1), 31-35.

Ferreira, A. de Brum. 1978. Planaltos e montanhas do norte da Beira – estudo de geomorfologia. Centro de Estudos Geográficos, Lisbon, Portugal.

Gonzalez-Rabanal, F., Casal, M. 1995. Effect of high temperatures and ash on germination of ten species from gorse shrubland. Plant Ecology 116(2): 123-131.

Guerrero, C., Mataix-Solera, J., Arcenegui, V., Mataix-Beneyto, J., Gómez, I., 2007. Near-Infrared Spectroscopy to Estimate the Maximum Temperatures Reached on Burned Soils. Soil Sci. Soc. Am. J. 71(3), 1029-1037.

Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire. 18, 116-126.

Madrigal, J., Hernando, C., Guijarro, M., Vega, J. A., Fontúrbel, T.and Pérez-Gorostiaga, P., 2010. Smouldering fire-induced changes in a Mediterranean soil (SE Spain): effects on germination, survival and morphological traits of 3-year-old *Pinuspinaster*Ait. Plant Ecol. 208, 279–292.

McCarty, G.W., Reeves, J.B.III, Reeves, V.B., Follet, R.F., Kimble, J.M., 2002. Mid-infrared and near-infrared diffuse reflectance spectroscopy for soil carbon measurement. SoilSci. Soc. Am. J. 66, 640-646.

Moreira, B., Tormo, J., Estrelles, E., Pausas, J.G., 2010. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. Annals of Botany, 105, 627-635.

Otto, R., García-del-Rey, E., Muñoz, P. G., Férnandez-Palacios, J.M., 2010. The effect of fire severity on first-year establishment in a *Pinuscanariensis* forest on Tenerife, Canary Islands. Eur. J. Res. 129, 499-508.

Paula S, Arianoutsou M, Kazanis D, Tavsanoglu Ç, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A, Espelta JM, Palacio S, Fernández-Santos B, Fernandes PM, and Pausas JG. 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology 90, 1420.

Paula, S., Pausas, J.G., 2008. Burning seeds:germinative response to heat treatments in relation to resprouting ability. Journal of Ecology 96, 543-552.

Pausas J.G., Keeley J.E. 2009. A burning story: The role of fire in the history of life. BioScience 59, 593-601.

Pausas, J.G., Bradstock, R.A., Keith, D.A., Keeley, J.E. & GCTE Fire Network., 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*85, 1085-1100.

Pausas, J.G., Ouadah, N., Ferran, A., Gimeno, T., Vallejo, R., 2003. Fire severity and seedling establishment in *Pinushalepensis* woodlands, eastern Iberian Peninsula. Plant Ecol. 169, 205-213.

Pausas, L.G., Keeley, J.E., Verdú, M., 2006. Inferring differential evolutionary processes of plant persistence traits in Northern Hemisphere Mediterraneanfire-prone ecosystems. Journal of Ecology. 94, 31-39.

Pereira, P., Úbeda, X., Baltrėnaitė, E. , 2010. Mapping total nitrogen in ash after a wildland fire: a microplot analysis. Ekologija. 56 (3-4), 144-152.

Pérez, B., Moreno, J.M., 1998. Methods for quantifying fire severity in shrubland-fires. PlantEcology. 139, 91-101.

Rebollo, S., Pérez-Camacho, L., García-de-Juan, M.T., Benayas, J.M., Gómez-Sal, A., 2001. Recruitment in a Mediterranean annual plant community: seed bank, emergence, litter, and intra- and inter-specific interactions. OIKOS. 95, 485-495.

Rivas, M., Reyes, O., Casal, M., 2006. Influence of heat and smoke treatments in the germination of six leguminous shrubby species. Int. Journ. Wildland Fire. 15 (1), 73-80.

Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J,,Lousã, M., Penas, A., 2002. Vascular Plant Communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. ItineraGeobotanica 15(1), 5-432.

Rotundo, J.L., Aguiar, M.R., 2005. Litter effects on plant regeneration in arid lands: a complex balance between seed retention, seed longevity and soil-seed contact. Journal of Ecology. 93, 829-838.

Roy D.P., Boschetti L., Maier S.W., Smith A.M.S., 2010. Field estimation of ash and char colour-lightness using a standard grey scale. *Int. Journ. ofWildlandFire*19, 698–704.

Santos, A.S., 2010. Efeitos dos fogos florestais na dinâmica do azoto e carbono dos solos, na região centro de Portugal. M.Sc Dissertation.University of Coimbra, Coimbra.

Trabaud, L., 1992. From the cell to the atmosphere: an introduction to interactions between fire and vegetation. In Fire in Mediterranean ecosystems. Ecosystems Research Report. Trabaud L., Prodon R. (eds.) Commission of the European Communities. 5: 13-21. CEC, Brussels.

Tutin, T.G., Heywood, V.H., Burges, D.H., Valentine, D.H., Moore, D.M., Walters, S.M., Webb, D.A., 1964-1980. Flora Europaea. Cambridge UniversityPress, Cambridge.

Úbeda, X., Outeiro, L.R., Sala, M., 2006. Vegetation regrowth after a differential intensity forest fire in a Mediterranean environment, Northeast Spain. Land Degradation & Development. 17, 429-440.

Valbuena, L., Nuñez, R., Calvo. L., 2000a. The seed bank in *Pinus* stand regeneration in NW Spain after wildfire. Web Ecology. 2, 22-31.

Valbuena, L., Tárrega, R., Luis-Calabuig, E., 2000b. Seed banks of *Erica australis* and *Calluna vulgaris* in a heatland subjected to experimental fire. J. Veg. Sci. 11, 161-166.

Valbuena, L., Trabaud, L. 2001., Contribution of the seed bank to post-fire recovery of a heathland. Plant Ecology. 152, 175-183.

ViscarraRossel, R.A. Walvoort, D.J.J., McBratney, A.B., Janik, L.J., Skjemstad, J.O., 2006. Visible, near infrared, mid infrared or combined diffuse reflectance spectroscopy for simultaneous assessment of various soil properties. Geoderma 131:59–75.

Wohlgemuth, P., Hubbert, K., Arbaugh, M., 2006. Fire and Physical Enviroment Interactions. In Sugihara, N., Wadgtendonk, J.W., Shadffer, K.E., Fites-Kaufman, J., Thode, A.E. Fire in California's Ecosystems. Regents of the University of California.

Zaller, J.G., Saxler, N., 2007. Selective vertical seed transport by earthworms: Implications for the diversity of grassland ecosystems. European Journal of Soil Biology.43, S86-S91.

**Chapter 4**

# Does fire change the seed bank below three Mediterranean shrub species with contrasting fire regeneration traits?

## Implications of seed dispersal patterns and fire effects for management

**Chapter 4**

**Does fire change the seed bank below three Mediterranean shrub species with contrasting fire regeneration traits? - Implications of seed dispersal patterns and fire effects for management**

*This chapter is in preparation for submission*

## Abstract

The main objectives of this study were to evaluate at what extent the community (pre-fire) seed bank was related with the standing vegetation and what would be the fire effects on the viability of the seed bank. Special focus was given to the implications of the seed bank of *E. umbellata* on the (fire) management of this habitat, due to its scarceness in the community and to the fact that it was the only obligate seeder.

Soil and litter samples from under the canopy of 3 shrub species (*Erica australis*, *Erica umbellata* and *Pterospartum tridentatum*) were collected before and after an experimental fire, over an area of 625 $cm^2$ (a 25*25 cm square). The shrubs were selected from 12 pre-established nearly regularly spaced points, within a 50*50 m plot. A total of 28 shrubs were sampled (12 *P. tridentatum*, 10 *E. australis* and 6 *E. umbellata*). Pre fire measurements included shrub height, diameter and litter volume collected. Temperature reached at 1,5cm depth was measured on the 12 locations. After fire, the minimum diameters of the burnt twigs and the volume of the ash (burnt litter) were measured. Pre and post-fire litter and soil samples were put to germinate in a greenhouse for 10 months, until no significant increase of germination was recorded.

The seed densities of *Erica umbellata* and *Erica australis* were noticeably high under the same species canopies. Contrastingly, the density of *P. tridentatum* seeds was equally low under its canopy or under the other shrubs. Both pre-fire as the post-fire soil seed bank were dominated by *Erica australis* and *E. umbellata* seeds; *P.*

*tridentatum* seeds were extremely underrepresented in the seed bank, despite being the dominant species in the vegetation.

*Erica australis* and *E. umbellata* seed density suffered a noteworthy reduction in the litter layer, mostly attributed to the litter combustion. *P. tridentatum* suffered no marked reduction, but this was primarily due to extremely low germination densities from the pre-fire samples.

The overall germination from the soil seed bank showed no global effects of fire, however, the heterogeneous temperatures achieved by fire stimulated germination in some parts, while hampering the seed bank in others. This was particularly clear for *E. australis*, with fire-induced changes in germination significantly related with the temperature achieved in the soil.

The results show no evidence that the use of fire as a management tool, at the current frequency, implies an imminent high risk of decline of the *E. umbellata* population; even though the adult shrubs are scarce in the landscape, its seed shadow goes much beyond the mother plants.

Keywords: *Erica umbellata, Erica australis*, *Pterospartum tridentatum*, heathland, soil seed bank, indirect method, experimental fire, temperature.

### 4.1. Introduction

Heathlands and shrublands currently occupy extensive areas of the Mediterranean region, covering a total surface of over 110.000 km2 (Calvo et al. 2012). These formations are typically affected by fires, and, in Portugal, represent the most fire-prone land-cover type (Silva et al. 2009). While heathlands are treated as important ecosystems for nature conservation in Northern Europe, in the Mediterranean they are generally regarded as marginal lands with low productivity and economic value, often representing a degradation state of the climax vegetation (Calvo et al. 2012).

Nonetheless, Mediterranean heathlands and shrublands are increasingly recognized to provide key ecosystem services, especially related to traditional products from grazing by sheep and goats and bee keeping.

Mediterranean heathlands are mainly composed of Ericaceae (*Erica* and *Calluna* genera) and, to a lesser degree, by Leguminosae and Cistaceae. These families are well-adapted to fire-prone environments, since they present traits that allow them to cope with repeated fires, persisting after fires at the level of individual plants by re-sprouting (resprouters) and/or at the population level through an in-situ seed bank (seeders) (Paula & Pausas 2008).

The community of study is composed by shrub species with contrasting fire-regeneration strategies. *Pterospartum tridentatum* (L. Willk) is the dominant species. It belongs to the Leguminosae family and is a strong resprouter with post-fire enhanced germination potential (Valbuena & Vera, 2002; Vasques et al., 2012). *Erica australis* (L.) and *Erica umbellata* (Loefl. ex L.) are the main Ericaceae shrubs in the area. These two species have contrasting post-fire regeneration strategies. *E. australis* is a resprouter (Paula & Pausas 2008; P. Maia et al. 2012), with potential post-fire germination stimulation ( Cruz et al. 2003; Vasques et al. 2012). In turn *E. umbellata* is an obligate seeder, and although heat has been reported as a poor germination stimulus (Vasques et al. 2012), smoke exposure showed to greatly increase germination percentage and even seedling growth (Moreira et al. 2010).

Some studies have considered the main seed dispersal mechanism of *Pterospartum tridentatum* to be autochory (Valbuena, Nuñez, & Calvo, 2001; Valbuena & Trabaud, 2001), but seed morphology, particularly the presence of an elaisome, may indicate potential for secondary dispersal by ants (myrmecochory) (Lopez 2000). Anemochory is held to be the main seed dispersal mechanism of both Ericaceae species, due to the small seed size (Trabaud, 1994;Valbuena & Trabaud, 1995, 2001). However, because of the closed structure of the shrubland (gaps or herbs cover were practically inexistent), the main process in primary seed dispersal was assumed to be vertical

seed rain, at a close distance from the mother plants, since wind dispersal patterns should be disrupted by the closed structure of the canopy (Bullock and Moy 2004; Chambers and MacMahon 2011). In this sense, the density of seeds of given species, in the soil seed bank, was expected to be higher under its own canopy than in other locations. As a consequence, the probability of post-fire recruitment of a species would be higher in the patches under the same species shrubs; if intra-specific competition (e.g. auto-inhibition of germination caused by litter) does not play an important role (Bonanomi et al. 2005).

Post fire spatial variability in soil seed banks and soil seed bank richness patterns have been studied in several woodland ecosystems (Eshel et al. 2000)Torres, et al, 2013). The study of Eshel, Henig-Sever, and Ne'eman (2000) focused on the recruitment of *Pinus halepensis* and *Cistus* spp. around burnt mature pine trees. They found that, in the case of pines, the seedling recruitment decreased with increasing distance from the mother plant, and that herbs and shrubs were recruited mostly on gaps and shrub patches. The study of Torres et al, (2013) showed that, while soil seed banks of herbs were spatially related to the patterns in the vegetation, the soil seed bank of woody shrubs was not. However, no studies were found dealing with the fine scale soil seed bank patterns in relation to the canopy shrub species. This is an important aspect to consider in fire-prone shrub communities, since the patterns in the soil seed bank influence the post-fire regeneration of the community (Valbuena and Trabaud 2001; Orscheg and Enright 2011), and provide the main source of regeneration for obligate seeders that do not form aerial seed banks.

Experimental fires are an extraordinary opportunity for understanding the changes caused by fire in the ecosystems. As opposed to wildfires, that are mostly unpredictable, experimental fires make possible the repeated sampling in previously chosen locations, and additionally they permit the installation of devices or the measurement of pre fire parameters that can be used to estimate fire severity (Pérez &

Moreno 1998; Hutchinson et al. 2005; Moreno et al. 2004). Wildfire scenarios don't normally permit this kind of methodological design, and assumptions of the pre-fire situation are done by comparing with control plots. These are normally established in the unburnt, neighbouring areas, with putative similar characteristics, which nonetheless may result in uncertainty as to the actual effects of fire (e.g. Ferrandis, Herranz, & MartinezSanchez, 1996; Maia et al., 2012).

In communities, like the one studied here, where seeders are clearly dominated by resprouters, the post-fire community composition may progress in a direction where seeders tend to be less abundant (Calvo, Tárrega, and Luis 2012), and eventually disappear at the local scale. High recovery of the vegetation due to resprouting of the dominant species, can leave little opportunity for *E. umbellata* seedlings to establish, mature and produce seeds ((Rego, et al., 1991; Fernández, et al., 2013b). The risk of local extinction then increases with increasing fire recurrence, given that soil seed banks may become exhausted (e.g. Ferrandis, Herranz, and Martinez-Sanchez 1999; Ottewell et al. 2009). The understanding of the post-fire vegetation dynamics, particularly in respect to fire-interval, is essential in these ecosystems, that are often managed by prescribed fires, for decreasing wildfire risk or creating pastures for grazing (Fernandes et al. 2013).

This study intends to analyze how fire affects the potential for the community to regenerate by germination, which is the only regeneration strategy of *E. umbellata*.

The specific hypotheses are:

1. The species of the above ground vegetation are well represented in the seed bank (Bossuyt & Honnay 2008). Specifically, it is expected that the density of seeds (on the litter and in the soil) of a certain species is higher under the same species canopy, than in other locations.

2. The impact of fire on the seed bank depends on fire severity and maximum temperature reached in the soil. The germination of *Erica umbellata*, an obligate

seeders is expected to be more stimulated by fire than the germination of E. australis or *P. tridentatum*.

## 4.2. Materials and Methods

### 4.2.1. Study Site

The study site was a heathland located in Central Portugal, near Castanheira de Pêra. The habitat characteristics fall under the classification of European heathland (type 4030), subtype 4030pt3 – "heathlands with dominance or co-dominance, with different combinations, of *Erica umbellata, Erica australis* subsp. *pl., (…) Pterospartum tridentatum* subsp. *pl. (…)".*(Aguiar & Capelo 2000, ICNF 2013).

The study site comprises a series of plots where experimental fires have been carried out during the last decade. The plot studied here had not been burned for 8 years (Viegas, D. X., pers.comm.). The plot was approximately 50 m x 50 m, had a slope angle of 8 % and NE aspect. By the time of this study, the plot's fuel load was estimated at 35 ton/ha. It presented a continuous cover of shrub vegetation, with no bare soil or grass cover. *Pterospartum tridentatum* was the species that most contributed to this cover (>60%), followed by *Erica australis* (~30%) and sparse individuals of *Erica umbellata* (<10%). The cover of other woody species, like *Halimium* spp. and *Cistus* spp. was not representative in the plot, although they were present in the vicinities.

### 4.2.2. Experimental lay-out and field sampling

In the study plot, 12 sampling points were established in a grid layout but excluding the plot's bottom part because it revealed a markedly higher fuel load of dead *Erica* and was expected to suffer a comparatively high fire severity (**Figure 12**). At each sampling point, a thermocouple (EL-USB-TC, Lascar Electronics) linked to a data logger was

installed at a mineral soil depth of 1.5 cm. Temperature data were stored at 4-seconds intervals but, unfortunately, two thermocouples produced aberrant data. Within a 1.5 m radius from each thermocouple, 1 specimen of at least two or, if present in the area, of the three of the plot's dominant shrub species (*Pterospartum tridentatum*, *Erica australis* and *Erica umbellata*) was selected. Even though the distance between the selected shrubs was small, the overlap area between their canopies was minimal. As illustrated in **Figure 12**, in total 12 *P.tridentatum*, 10 *E. australis* and 6 *E. umbellata* specimens were selected. The experimental fire took place in the 6th of May, 2010; the previous experimental fire had occurred 8 years before.

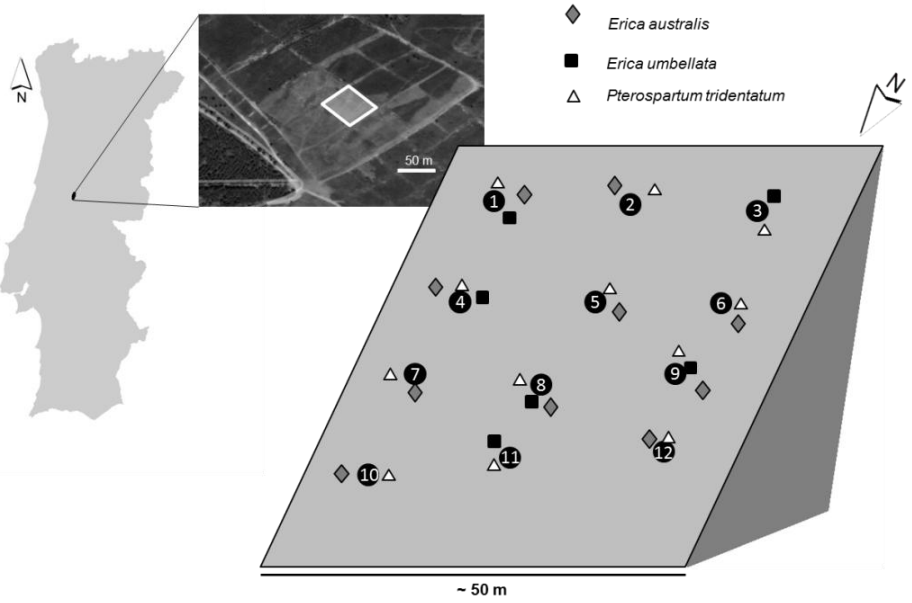



**Figure 12** – Location of the study site and plot as well as schematic view of the experimental set-up comprising 12 sampling locations with two or three target plants and equipped with thermocouples.

Before the experimental fire, the selected plants were described in terms of height and canopy diameter, and sampled with respect to the seed bank below their canopies. To this end, the litter layer and upper 3 cm of the mineral soil were collected separately over a square area of 625 $cm^2$ (a 25*25 cm square). This sampling area was positioned

such that one of its corners coincided with the center of the canopy, and was marked with pins at the three other corners to avoid overlap in pre- and post-fire sampling areas.

Immediately after the fire, the ash layer ("ash" samples are often a mixture of unburnt, scorched and burnt litter and ashes. Hereafter it will be referred to as "ash") and the upper 3 cm of the mineral soil were collected separately as well from an adjacent square area of 625 $cm^2$.

Furthermore, the diameters of the thinnest 5 branches of each specimen were measured at 1 cm below the tip of the branch (see Maia et al. 2012 (a, b)).

#### 4.2.3 Seed bank assessment

Although the direct method (direct observation of the seeds in the sample) for seed bank assessment, after sieving and washing the sediment was considered as adequate for estimating densities of seeds with distinct morphology (Gross 1990) this would further imply viability testing of the seeds which, taking into consideration the small size of the seeds and high densities expected would be impracticable in the framework of this work. Hence, the indirect method (seed bank analysis through germination), proven to be adequate for the first 5 cm of soil (Price et al. 2010) was chosen since the objective was to evaluate the impact of fire in the viable portion of the seed bank, which influences the post-fire community.

The litter, ash and soil samples were transported to a greenhouse, where the bigger rocks and wood debris were removed manually before measuring the volumes of the litter and ash samples. Each individual sample was then spread over a 3 cm thick layer of vegetable substratum in an aluminum tray that had been perforated to allow for water drainage. In addition, 15 trays containing only turf were also placed in the greenhouse, in order to control for possible weed contamination.

All 127 trays were then placed in a greenhouse on 29 may 2010 for a period of 10 months under ambient temperature and natural photoperiod. The germination trays

were watered as needed, by means of sprinklers connected to an artesian well. The seedlings that emerged in each tray were counted at 1- to 2- weekly intervals, and were all marked with metal pins to avoid double counts. The seedlings were removed as soon as they could be identified, whereas the remaining seedlings were transplanted to individual pots to allow growth and subsequent identification. During the experiment, the individual trays were also photographed at monthly intervals to have a documented record and, if needed clarify possible doubts about species identification.
Unfortunately, since 5 trays suffered an accident at the beginning of the experiment, the final dataset consisted of 122 trays, In a few cases, species identification of *Erica* seedlings was not possible due to seedling mortality, so those samples could not be included for *Erica australis* and *E.umbellata* statistics.

#### 4.2.4. Data analysis

The explanatory variables used for the pre-fire seed bank were plant height, diameter, and litter volume. For the post-fire seed bank, the following fire-related variables were also considered: minimum Twig Diameter, maximum temperature reached during the fire, as measured by the thermocouples, (only 10 out of the 12 devices worked correctly) ash volume and consumed litter volume (litter-ash volume).

The Latin binomial nomenclature was used when analyzing germination densities and seed bank, or when describing characteristics of the target plants. When referring to samples or sampling locations, a three letter code was used instead, unless specifically mentioned otherwise. (code: EAU – *Erica australis*, EUM – *Erica umbellata*, PTR – *Pterospartum tridentatum*).
Data analyses were carried out with IBM SPSS version 19. Assumptions for parametric analyses could not be met, even after standard data transformations.

Comparison of densities of *Erica australis*, *E. umbellata* and *P. tridentatum* seedlings, between the three sampling locations (EAU, EUM, PTR), were done with the Kruskal-Walis non-parametric test. *Post hoc* pairwise comparisons were carried out using the Mann-Whitney U-test in the individual pairs, correcting α by the Holm's sequential Bonferroni method (Holm, S. 1979).

The differences between pre- and post-fire germination densities, for each individual sampling point, were analyzed through the Wilcoxon paired-samples test.

The Spearman correlation coefficient was used to test the relation between pre-fire seed bank data and pre-fire vegetation measurements. The relation between post-fire seed bank and pre fire vegetation measurements, as well as fire severity measurements was also tested. Besides this, the relation between the fire-induced changes in seedling density and the severity indicators was also tested, for the different target species.

## 4.3. Results

### 4.3.1 Before the experimental fire

#### Pre-fire seed bank

Litter

The germination of the seeds from the litter samples revealed a poor relation with the canopy species. *Erica australis* was more abundant under EAU (208±407 seedlings.m$^{-2}$) and PTR (213±341), than under EUM (0±0 seedlings.m$^{-2}$), but the differences were not statistically significant (p>0.1) (**Figure 13**). *E. umbellata* had higher density under EUM shrubs (858±1120seedlings.m$^{-2}$) than in the samples collected under EAU (183±469 seedlings.m$^{-2}$) or PTR (125±120 seedlings.m$^{-2}$), but also without statistically significant differences (p>0.1). On its turn, *P. tridentatum* was similarly (p>0.1) scarce,

under its own canopy (PTR 8±13 seedlings.m$^{-2}$) or on other locations (under EAU 2±5seedlings.m$^{-2}$), under EUM (5±8 seedlings.m$^{-2}$).

Soil

The seedbank of the topsoil revealed a clearer association with the canopy species,at least in the case of the two *Erica* spp.. *E. australis* germination was significantly higher in the samples collected under its canopy than anywhere else (989±675seedlingss.m$^{-2}$ under EAU vs 312±343seedlings.m$^{-2}$ under EUM and 231±261seedlings.m$^{-2}$ under PTR; $p< 0.05$). An analagous pattern was found for *E.umbellata*, (597±533seedlings.m$^{-2}$ under EUM, vs 92±157 seedlings.m$^{-2}$ under EAU, vs 306±349 seedlings.m$^{-2}$under PTR), although it was not statistically significant ($p>0.1$) (Figure 2). *P. tridentatum* seedlings were scarce at all sample locations (14±18 seedlings.m$^{-2}$ under EAU; 5±8 seedlings.m$^{-2}$ under EUM and 14±19 seedlings.m$^{-2}$under PTR), hence not significantly different under the three species ($p>0.1$).

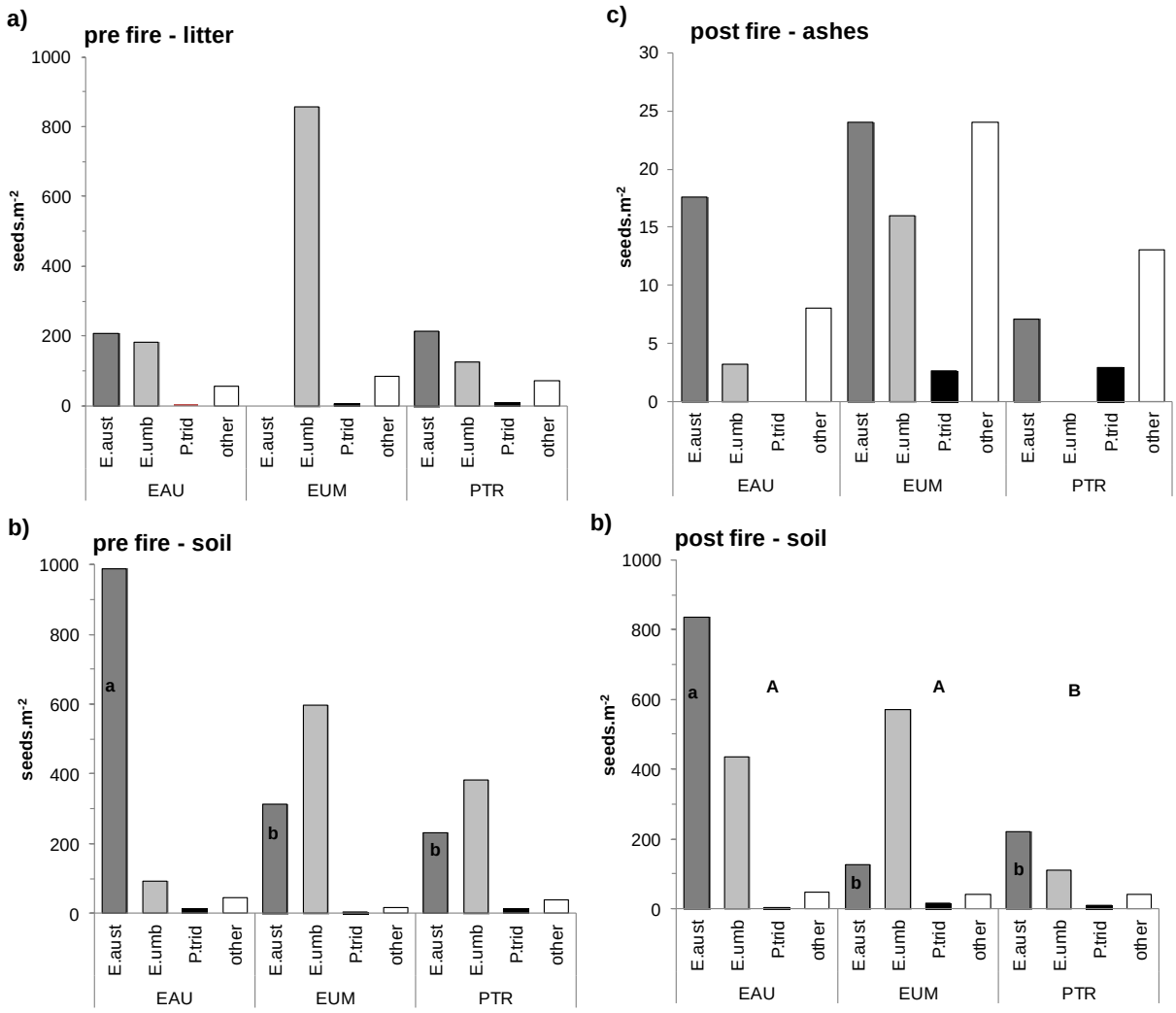



**Figure 13** –Germination densities from the litter and soil samples collected before (a and b) ad after the fire (c and d) below the canopy of the target species. Target species: EAU - *E. australis*, EUM - *E. umbellata*; PTR - *P. tridentatum*. Different lower case letters indicate statistically significant differences in seeds density (only occurring for *E. australis* seeds), between samples collected below the different target species' canopies. Different capital letters indicate statistically significant total seeds density between target species samples – bars not shown. Note the difference in the y-axis scale on c) – max 30.

## Relation of pre fire seed bank with plant size and litter volume

Shrub size was species dependent. *E.australis* shrubs were the largest, both in height and diameter, whereas *E.umbellata* shrubs were the smallest. *P.tridentatum* shrubs had a median height but a large canopy diameter (**Table 5**).

**Table 5–** Pre and post fire characteristics of the sample points. Mean values and (standard deviations). Different letters mean statistically significant differences (p<0.05, p<0.1 indicated *italic*) between species, tested trough Kruskall-Wallis.

| | | | ***Erica australis* (n=10)** | | ***Erica umbellata* (n=6)** | | ***Pterospartum tridentatum* (n=12)** | |
|---|---|---|---|---|---|---|---|---|
| | | | mean (sd) | | mean (sd) | | mean (sd) | |
| **a)** | **Pre Fire** | Plant Height (cm) | 148 (27) | (a) | 92 (24) | (b) | 102 (19) | (b) |
| | | Canopy Diam (cm) | 146 (36) | (a) | 83 (36) | (b) | 118 (37) | (a) |
| | | Litter Volume (ml) | 1520 (424) | | 1483 (392) | | 1817 (478) | |
| **b)** | **Post Fire** | TSI | 10,7 (3,25) | (a) | 9,6 (4,13) | (a) | 5,8 (2,21) | (b) |
| | | volumeASH | 435 (182) | (a) | 275 (197) | (*b*) | 475 (463) | (a) |
| | | volLitter_VolumeAsh | 1085 (379) | | 1208 (412) | | 1342 (615) | |
| | | Max Temperature (ºC) | | | 44 (17) | | | |

The seed density in the litter was related to the canopy size but the relation was not the same for the three target species. The seed bank of *E. umbellata* was significanty related to the canopy diameter of EUM shrubs (ρ=0.975; p<0.05), its density increasing with increasing canopy diameter. Such a positive relation was also suggested for *P.tridentatum*, but it was only marginally significant (ρ=0.588; p<0.1). By contrast, the density of *E. australis* seedlings appeared to be negatively related with the height of the EAU shrubs before the fire (ρ= -0.676; p <0.1) (**Table 6**).

**Table 6** – Spearman correlations between **a)** pre fire measures, **b)** post fire measures and pre-and-post fire seed bank densities. Only seed banks of the target species are considered. Target species – EAU – *Erica australis*, EUM – *E. umbellata*, PTR – *Pterospartum tridentatum*. *P* values lower than 0,1 are marked with ~*s*, lower than 0,05 with *.

**a)** **PRE FIRE VEGETATION**

| | | | LITTER / ASH | | SOIL | |
|---|---|---|---|---|---|---|
| | **Target Species** | **N** | **Height** | **Canopy Diam** | **Height** | **Canopy Diam** |
| **Pre-Fire Seed Bank** | EAU | 8-10 | -0,676 ~*s* | -0,512 *n.s* | -0,132 *n.s* | 0,117 *n.s* |
| | EUM | 5 | 0,308 *n.s* | 0,975 * | 0,316 *n.s* | 0,300 *n.s* |
| | PTR | 9-10 | 0,230 *n.s* | 0,588 ~*s* | -0,184 *n.s* | -0,525 *n.s* |
| **Post-Fire Seed Bank** | EAU | 9-10 | 0,167 *n.s* | 0,035 *n.s* | 0,174 *n.s* | -0,051 *n.s* |
| | EUM | 5-6 | 0,135 *n.s* | -0,133 *n.s* | -0,103 *n.s* | -0,359 *n.s* |
| | PTR | 12 | -0,216 *n.s* | -0,338 *n.s* | 0,282 *n.s* | 0,338 *n.s* |

**b)** **MAX. TEMPERATURE AND FIRESEVERITY**

| | | | ASH | | | SOIL | | |
|---|---|---|---|---|---|---|---|---|
| | **Target Species** | **N** | **Max Temp.** | **Twig Diam** | **Ash Volume** | **Max. Temp.** | **Twig Diam** | **Ash Volume** |
| **Post-Fire Seed Bank** | EAU | 7-10 | 0,273 *n.s* | -0,038 *n.s* | 0,252 *n.s* | -0,786 * | -0,561 *n.s* | 0,420 *n.s* |
| | EUM | 4-6 | - - | -0,131 *n.s* | 0,393 *n.s* | -0,400 *n.s* | -0,900 * | 0,900 * |
| | PTR | 10-12 | -0,174 *n.s* | -0,097 *n.s* | 0,099 *n.s* | 0,130 *n.s* | -0,002 *n.s* | 0,594 * |

### 4.3.2. After the experimental fire

#### Post-fire seed bank

Ash

The germination from the ash layer, like that from the pre-fire litter layer, showed a poor association with target species, in the sense that seedlings densities were not significantly higher under the shrubs of the same species than under those of the other species. An exception was *E. umbellata,* revealing three times more seedlings under the own canopy (16 ± 39 seedlings.$m^{-2}$) than under EAU (3 ± 10 seedlings.$m^{-2}$ ) and no seedlings under PTR. However, the differences in seedling density, from under the same species canopy and other locations was in no case statistically significant ($p>0.1$) (**Figure 13**).

Soil

The soil seed bank was more concordant with the target species. The density of *E.australis* seedlings was significantly higher under EAU (835 ± 989 seedlings.$m^{-2}$) than under EUM (127 ± 161 seedlings.$m^{-2}$) or PTR (221 ± 336 seedlings.$m^{-2}$) ($p<0.05$) (**Figure 13**). An analogous tendency was observed for *E.umbellata* seedlings, but differences were not statistically significant ($p>0.1$). The soil seed bank of *P. tridentatum* was practically zero under all three target species and, thus, did no vary in a significant manner ($p>0.1$) (**Figure 13**).

#### Relation of post-fire seed bank with pre-fire seed bank and fire severity indicators

In general, the measurements performed before the experimental fire (shrub height, canopy diameter, litter volume) had no influence on the post-fire germination of both the ash and soil samples (**Table 6** a). The germination from the ash samples was also

unrelated to the fire severity indicators (**Table 6**c). By contrast, post-fire germination from the soil samples appeared to be related with fire severity (**Table 6**b).

The density of *P.tridentatum* seedlings in the soil was positively correlated with the volume of remaining ashes under PTR ($\rho$=0.59; $p<0.05$), suggesting that germination from the soil seed bank was hindered by increasing fire severity. Likewise, *E. umbellata* density was positively related to the volume of ashes under EUM and, in addition was, negatively related to the diameter of the remaining twigs. The density of *E.australis* seedlings was negatively related with the maximum temperature recorded at 1,5 cm depth (**Table 6**b(soil)), also an indication that germination was inhibited by increasing fire severity.

### 4.3.3. Fire-induced changes in seed bank

Fire markedly decreased the density of seedlings germinating from the litter samples (litter - 601±689 vs ash - 44±52 seedlings.m$^{-2}$)($p<0.001$). This was true for both *Erica* species, but when considering the samples under the respective target species, it was marginally significant onlyin the case of *E. umbellata* (litter-858±1120 vs ash-16±39 seedlings.m$^{-2}$ ($p=0.068$) (*E. australis* – litter-208±408 vs ash-18±24 seedlings.m$^{-}$2; $p>0.1$). (**Table 7**).

**Table 7** – Pair-wise comparison between pre-fire and post-fire seedlings density from the litter and soil samples, for all sampling points, and for the samples under the target shrubs. Symbols: ↑- overall increase, ↓ - overall decrease, ↔ - no overall significant changes.

| | | | LITTER / ASH | | | SOIL | | |
|---|---|---|---|---|---|---|---|---|
| | | | mean (sd) | | Overall difference (*p*) | mean (sd) | | Overall difference |
| TARGET | seed bank density (seed.m$^{-2}$) | N | pre fire | post fire | | pre fire | post fire | |
| all | *E.australis* | 21 | 167 (333) | 15 (29) | ↓ (0,038) | 564 (598) | 432 (701) | ↔ |
| | *E.umbellata* | 21 | 299 (621) | 5 (20) | ↓ (0,001) | 306 (377) | 327 (405) | ↔ |
| | *P.tridentatum* | 25 | 5 (10) | 2 (5) | ↔ | 12 (16) | 9 (20) | ↔ |
| | Total | 25 | 601 (689) | 44 (52) | ↓ (<0,001) | 1105 (696) | 1008 (863) | ↔ |
| EAU | *E.australis* | 9 | 208 (408) | 18 (24) | ↓ n.s. | 989 (675) | 835 (989) | ↔ |
| EUM | *E.umbellata* | 5 | 858 (1120) | 16 (39) | ↓ (0,068) | 597 (533) | 571 (605) | ↔ |
| PTR | *P.tridentatum* | 9 | 8 (14) | 3 (6) | ↔ | 14 (19) | 9 (23) | ↔ |

N is the valid number of pairs available for the test; a valid pair is the pre-fire and post-fire samples for the same sampling point and layer.

The exception to this pronounced fire-induced decrease in germination was *P. tridentatum*, which showed an unclear pairwise comparison pattern between the litter and ash samples – (4 ties, 2 increases and 3 decreases ($p>0.1$) maintaining similar mean density values before (8±14 seeds.m$^{-2}$) and after fire (3±6 seeds.m$^{-2}$) ($p>0.1$) (**Table 7**).

The experimental fire did not produce significant changes in the overall germination densities from the soil seed bank ($p>0.1$). The absence of a significant impact was equally observed for each of the individual target species, from under their respective target shrub ($p>0.1$) (Table 3).

Nonetheless, there was some suggestion that fire resulted in differential effects on the germination from the seed bank, depending on the maximum temperatures measured in the soil, at 1.5 cm depth.

In the case of *E. australis*, germination seemed to be increasingly enhanced with increasing temperatures up to 42.5 ºC, but increasingly inhibited by higher temperatures (**Figure 14**). In general, the differences in post- and pre-fire densities of *E. australis* seedlings under EAU shrubs were negatively related with the maximum recorded temperatures ($\rho$=-0.825, p=0.023; N pairs =7). In particular, there was a positive relation with temperature and germination density up to 42.5ºC (N = 3; $\rho$=1; p=0.019) and a non-significant negative relation for higher temperatures (N=4; $\rho$=-0.85; p>0.1).

In the case of *E. umbellata*, the available data is very limited due to sensor failure and lower initial sample numbers (lower density of adult shrubs (**Figure 12**, **Figure 14**).

*P. tridentatum* was consistent in showing no apparent sensitivity to fire, for any of the recorded temperatures, when compared with the *Erica* spp. Notwidstanding, the low mean germination densities from the pre-fire samples that recorded higher burn temperatures, severely limited the analysis of fire effects on the germination.

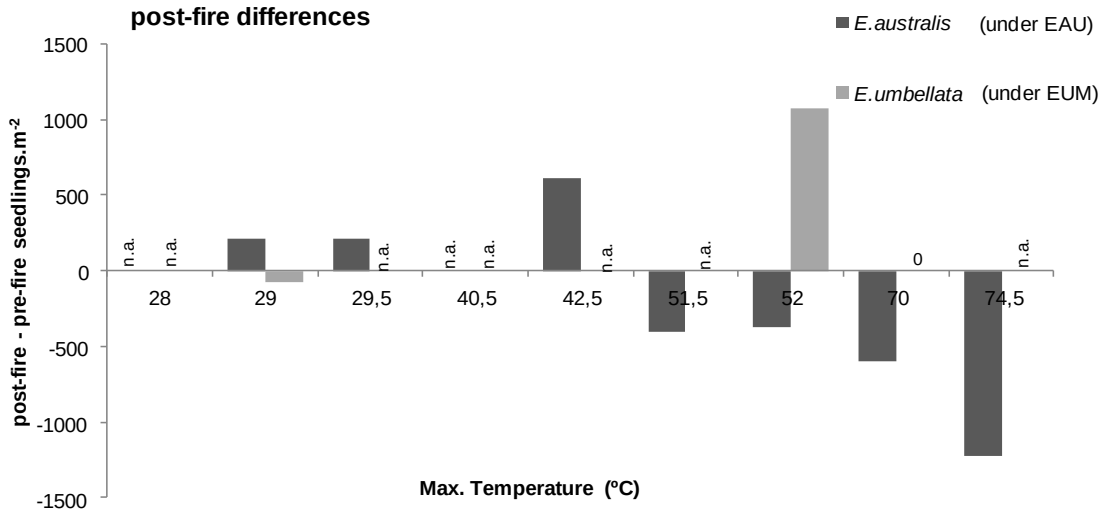



**Figure 14** – Differences in germination density, along a gradient of Maximum Temperature recorded by the thermocouples. The values correspond to absolute density differences (post-fire – pre-fire), for each target species, considering the samples collected under the respective target shrub. Only 10 of the 12 devices worked correctly. Δ seedlings.m$^{-2}$(*E. australis*) was sign. correlated with max. temperature (ρ=-0.825, p=0.023; N pairs =7).

## 4.4. Discussion

### 4.4.1. Seed bank variability in relation to vegetation characteristics and species dispersal mechanisms

The litter as well as topsoil seed bank of this community was clearly dominated by *Erica australis* and *Erica umbellata*, in spite *Pterospartum tridentatum* was the dominant species in the above-ground vegetation.

A study conducted in a heathland, dominated by *Erica australis*, in north Spain (Valbuena & Trabaud, 2001), showed very similar seed bank densities than the present study (unburnt=1050 seeds.m$^{-2}$), but, unlike in this study, the germination from the soil seed bank did not exhibit the dominant species found in the vegetation. They have attributed this to low viability of the seeds or to high dormancy levels which did not allow observation of seedling germination, for the duration of the germination

experiment (17 months). The fact that both studies were indirect analysis of the soil seed bank makes difficult to unravel the different dynamics between seed bank and standing vegetation.

In the present study, the dominant species of the vegetation were found in the seed bank, and moreover, seed densities of both *Erica australis* and *E. umbellata* were more abundant under canopies of the same species than in other locations, at least in the soil layer. This was expected, since a) In the absence of wind, it is expected that the seeds are dispersed by gravity and b) the closed structure of the canopies could disrupt wind dispersal (Bullock & Moy 2004). In fact, wind can be an overestimated agent of seed dispersal (Bakker & Berendse 1999); a study of the dispersal patterns of *Calluna vulgaris* showed that, even in the absence of vegetation that could disrupt wind dispersal, most seeds fell within 1 m from the mother plant (Gilbert & Butt 2010).

Variability in seedlings density was much higher in the litter than in the soil, amounting to twice as high the mean values. This higher variability found in the litter seed bank was probably, the reflection of the higher seed input by primary seed dispersal, and on the other hand, of the higher mortality rates in the litter than in the soil. The litter seed bank is the main recipient of primary dispersion, but contrastingly, seeds and seedlings there may experience higher mortality risks than in the soil (Chambers & MacMahon 2011; Nathan & Muller-landau 2000). Most of the seedlings that germinate in the litter layer may fail to survive, as emerging through the litter layer or establishing an effective contact with the soil may be a challenge for seedlings (Denham et al. 2009; Facelli & Pickett 1991).

Despite the limitations in considering the litter as an effective seed reservoir, the relations between the number of seeds of *E. umbellata* and *E. australis* in the litter beneath their canopies may elucidate about the “health” of both populations and contrasting realtions between seed production and plant age. The litter seed bank layer of *E. umbellata* was significantly and positively correlated with canopy diameter,

contrastingly, the litter seed bank of *E. australis* was (almost significantly) negatively related with shrub height. This could be explained by the different age of both populations - *E. umbellata* individuals are young plants, resulting from post-fire cohorts, while *E. australis* population is mostly composed by mature shrubs, that probably suffered repeated disturbances and whose vigor, both vegetative and sexual was, probably, decreasing ( Cruz & Moreno, 2001; Fernández, Vega, & Fonturbel, 2013).

The small amount of *P. tridentatum* germinating from the soil seed bank has been seen elsewhere: in a pine woodland, where it was present in the understory (P. Maia et al. 2012) and in a heathland, where it was dominated by Ericaceae shrubs (Valbuena & Trabaud, 2001). However, in the present study, *P. tridentatum* was the dominant species in the vegetation and was also a target species for the soil seed bank sampling, but despite that, its density was similarly low. The low density of *P. tridentatum* in the seed bank, compared to those of *Erica* spp. can partially be explained by 1) lower seed production potential added to 2) higher predation of its seeds due to larger size, and hence, higher nutritious level. Predation of this species seeds can be very intense even before maturation, particularly by weevils (author's personal observation), which has been observed for other Leguminosae species (e.g. Podlussány, Jermy, & Szentesi, 2001; Rodriguez, Peco, & Gurrea, 2011).

The lack of *P. tridentatum* seeds under its canopy, contrasting to the observed for both *Erica* spp, is an indication of the potential for myrmechocory as a secondary dispersal mechanism, similarly to other Leguminosae species bearing an elaisome (Lopez 2000). This secondary seed dispersal mechanism, allied to low seed production, would explain the small numbers of *P. tridentatum* seeds found under its canopy, where seed numbers were expected to be higher than in other locations. Additionally, the overall poor seed bank of this species could also be attributed to high predation rates, namely by ants (Nathan and Muller-landau 2000, Hughes and Westoby 1990).

### 4.4.2. Fire-induced changes in the soil seed bank

This study did not observe overall fire effects on the germination from the soil seed bank, at the slope scale; neither in relation to total species density nor in relation to the density of the target species. Rather than implicating that fire carried no impact in the soil seed bank, this means that, even in a small plot like the one studied here (50 x 50 m), temperature achieved by fire can be heterogeneous, promoting germination at some locations while inhibiting it at other locations.

A differential role of fire severity was also observed in the soil seed bank of a Maritime pine stand, which understory was dominated by *Erica* spp., *Calluna vulgaris* and *P. tridentatum*. In this case post-fire seedling densities were not much different than in the unburnt (control) area, but that was due to an increase in germination densities in the low severity areas, counterbalanced by a decrease in the high severity patches (Maia et al. 2012).

There was a remarkable decrease in germination density caused by fire in the litter layer. However, due to the potential for seedling mortality in the litter layer (Denham et al. 2009; Facelli & Pickett 1991), this may carry limited consequences for the post-fire community regeneration.

The fire severity indices analyzed by this study did not explain consistently the post-fire germination of the three target species and did not explain the overall fire-induced changes in the soil seed bank. The exception to this was *Erica australis*, which fire induced changes in germination density were related with the maximum temperature recorded, unlike what was observed by Férnandez, et al. (2013), that found no relation of *E. australis* germination and temperature caused by fire. Inter-population variability, may explain differences in post-fire germination behavior of this species (Cruz et al. 2003; Vasques et al. 2012).

The maximum temperatures recorded in the present study, at 1,5 cm were very low (44±17ºC). However, considering the insulation promoted by the soil, it can be fairly

assumed that the temperatures achieved in the topmost soil layers were higher, as shown by Férnandez, et al. (2013), and then, more comparable with their study.

The overall germination of *E. umbellata* was not affected by fire, and the fire-induced changes in the germination of *E. umbellata* were not related with temperature or fire-severity estimates.

There was, however, a negative relation of the post-fire germination with fire severity, namely with the diameter of remaining twigs and the remaining volume of ash/litter on the soil. This is in agreement withpost-fire observations of *Erica* spp. germination from the soil seed bank of a pine forest (Maia et al. 2012). However, since the data available is so limited for mature *E. umbellata* shrubs, no strong conclusions can be drawn as to the actual effect of fire severity in this population.

Laboratory essays with *E. umbellata* reported extremely low germination percentage of this species (Moreira et al. 2010; Vasques et al. 2012). However, despite being the less abundant of the target species, the seed density of *E umbellata* was surprisingly high, even when all sampling points were taken into account. Nevertheless, this high densities of germination from the soil samples can be misleading as to the actual effect on community regeneration, as field observations of the germination of this species reported high seedling mortality (Quintana et al. 2004).

More remarkable is the disagreement between the present results of *P.tridentatum* and the germination percentages densities obtained by Fernández, Vega, and Fonturbel (2013b). They recorded 30 seedlings.m$^{-2}$ in the control samples and twice as much after an experimental fire. The present study revealed very low densities of *P. tridentatum* before fire, and showed no increase in germination density after fire.

Moreover, there are evidences that *P.tridentatum* seeds from a neighbouring population are stimulated by heat. A laboratory germination experimental conducted with seeds collected in the same region reported more than 40% increase in germination after heat exposure. While the present study, by evaluating the soil seed

bank indirectly, only addresses viable and non-dormant seeds, the fact that the post-fire germination densities were equally scarce than before the fire, strongly suggests that *P. tridentatum* seeds are being detained from entering the soil seed bank, either before dispersal from the legume (e.g. weevils - Podlussány et al., 2001) or by secondary dispersal (or predation) (Fox & Deveny 2006; Clarke & Campbell 2006).

### 4.4.3. Implications for management

In Portuguese territory, the community studied here is well conserved, and is not characterized by any rare or endangered species. This is an ecosystem utilized for herds, and fire is commonly used by shepherds for rejuvenating pasture quality. Amongst the threats to ecosystem conservation, increase in fire severity and or recurrence is the biggest concern, because of the associated soil erosion risks, and invasive species proliferation (Aguiar and Capelo year?). The present study found no seeds of invasive species in the soil seed bank. While no conclusions can be drawn as to erosion risk, it is likely that it would not be a major concern, given the considerable volume of litter still present over the soil after fire (Prats, S. et al., 2012, 2013).

Hence, from a conservational perspective, the major threat of increased fire frequency in this particular community would be the local extinction of *Erica umbellata*, given it is an obligate seeder in a community where it is clearly outcompeted by resprouter species. This suggestion is based on reported trends on the post-fire decline of *E.umbellata* and species with comparable regeneration types in similar habitats (Céspedes et al. 2013; Férnandez, et al., 2013a; Fernández-Abascal et al. 2004; Rego et al., 1991). A study conducted in a close heathland found, that in a 4 year period, the post fire cover values of *Erica australis* and *Pterospartum tridentatum* increased in relation to the before the fire, and that *E. umbellata* decreased (Céspedes et al. 2013). Similarly, other studies in Spain reported increased post fire cover of *Erica australis* ,

but decreased post-fire cover of *Calluna vulgaris* (Fernández-Abascal et al. 2004). Considering that *Calluna vulgaris* has comparable habit and reproductive strategies to *E.umbellata*, this study may elucidate on the possible trends for the present study area, as well as corroborate this dynamics for different communities.

However, prescribed fires could be used as a management tool, e.g., for fire hazard reduction, without compromising the community composition. The present data shows no evidences of the eminent likelihood of the decline of *Erica umbellata* population; even though the adult shrubs are scarce in the landscape, its seed shadow goes much beyond the mother plants.

An important fact to bear in mind is that this experimental fire was conducted in the spring, when meteorological conditions were not propitious to high severity fires. Moreover, the last fire in the area occurred 8 years ago, which allowed for an abundant formation of *Erica umbellata* seed bank, notwithstanding its low cover values in the vegetation.

Fire interval is paramount, since in the eventuality of a second fire with a short interval, the depletion of the seed bank of this species would have, comparatively to the others that can regenerate vegetatively, the greatest negative consequence, because of the limited capacity for regeneration, and replenishing the seed bank. This basic principle applies for rare or endangered species (Vaughton 1998), that rely exclusively on germination for regeneration.

The review study by Bossuyt & Honnay, 2008 has shown that, among a wide variety of ecosystems, heathlands are the ecosystem which can better rely on the germination from the soil seed bank for post-disturbance community restoration.They have pointed out the overhelming dominance of Ericaceae seeds in relation to other species in the seed bank. The present study draws strong evidence in the same direccion; *P.tridentatum* is noticeably underepresented in the seed bank, comparatively to the Ericaceae species, despite being the dominant species in the vegetation. However, the strong resprouting ability of *P. tridentatum* will most certainly be the dominant

persistence mechanism of this species, probably mantaining its dominance in the landscape, unless post-fire mostarlity is high, or sprouting vigour is affected by fire.

Indeed, Fernández, Vega, and Fonturbel (2013b) have shown that high fire severity may reduce the resprouting vigour of *E. australis* and *P. tridentatum*, which has been also shown for other resprouter species of the Mediterranean basin (Moreira et al. 2012). These observations of the post-fire dynamics of resprouting, added to the potential for an abundant and long-living soil seed bank formation of *Erica umbellata* (Thompson & Band 1997), meet the requirements for the hypothetical use of low severity prescribed fires for the enhancement of *E. umbellata* population (Pyke, Brooks, & D'Antonio, 2010). This objective would be met if the post-fire mortality of the dominant resprouter species would create gaps for the successful regeneration of *E. umbellata* seedlings (see (Ooi et al. 2006). However, the mid-term survival of *Erica umbellata* seedlings can be very low (Quintana et al. 2004), which may imply serious consequences for the local persistence of this species, particularly if the potential recruitment is lowered by seed bank depletion caused by recurrent or more severe fires.

In any case, this is, prescribed fires for fuel reduction or improvement of pasture quality, or even the hypothetical use of fire as a restoration tool, early season fires would be preferable over late season fires, in relation to the effect in post-fire germination success of *E. umbellata* (Céspedes et al. 2013).

### 4.5. Conclusions

- *E. australis* and *E. umbellata* were well represented in the soil seed bank, being the dominant *taxa*. The representation of *P. tridentatum* in the soil seed bank was very low, despite being the dominant species in the standing vegetation.

- The density of *E. australis* soil seed bank was significantly higher under its canopy, and the same was suggested for *E. umbellata*. Contrarily, the density of *P. tridentatum* seeds was similarly low under its canopy or under the other shrubs. Seed predation

and secondary seed dispersal mechanisms, namely by ants may be playing a role in this.

- Overall fire effects on the soil were not obvious; however, the heterogeneous temperatures attained in the soil caused divergent effects over the plot – in some sampling points germination was increased, while in others was decreased. In particular, the differences of germination of *E. australis* were significantly related with maximum temperature recorded.

- *E. umbellata* soil seed bank was more abundant, but not limited, to the area under its canopy. In this sense, the use of prescribed burning, as a tool for the reduction of fire hazard and severity, should not imply the imminent risk for the decline of this species in the community, as long as fire interval permits plants to mature and replenish the seed bank.

**References**

Aguiar, C. & Capelo, J., 2000. Plano Sectorial da Rede Natura 2000 - habitats naturais.

Bakker, J. & Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in ecology & evolution, 14(2), pp.63–68.

Bonanomi, G., Legg, C. & Mazzoleni, S., 2005. Autoinhibition of germination and seedling establishment by leachate of Calluna vulgaris leaves and litter. Community Ecology, 6(2), pp.203–208.

Bossuyt, B. & Honnay, O., 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. Journal of Vegetation Science, 19(6), pp.875–884.

Bullock, J.M. & Moy, I.L., 2004. Plants as seed traps: inter-specific interference with dispersal. Acta Oecologica, 25(1-2), pp.35–41.

Calvo, L. et al., 2012. Post-Fire Management of Shrublands. In F. Moreira et al., eds. Post-Fire Management and Restoration of Southern European Forests. Managing Forest Ecosystems. Dordrecht: Springer Netherlands, pp. 293–319.

Calvo, L., Tárrega, R. & Luis, E., 2012. Changes of Species Richness in Heathland Communities over 15 Years following Disturbances. International Journal of Forestry Research, 2012, pp.1–12.

Céspedes, B. et al., 2013. Burning season effects on the short-term post-fire vegetation dynamics of a Mediterranean heathland T. O'Connor, ed. Applied Vegetation Science, p.n/a–n/a.

Chambers, J.C. & MacMahon, J.A., 2011. A DAY IN THE LIFE OF A SEED : Movements and Fates of Seeds and Their Implications for Natural and Managed Systems. Annual Review of Ecology and Systematics, 25(1994), pp.263–292.

Clarke, P.J. & Campbell, M.L., 2006. Seed dynamics of resprouting shrubs in grassy woodlands: Seed rain, predators and seed loss constrain recruitment potential. Austral Ecology, 31(8), pp.1016–1026.

Cruz, A. et al., 2003. Variability in seed germination at the interpopulation , intrapopulation and intraindividual levels of the shrub Erica australis in response to fire-related cues. , pp.93–103.

Denham, A.J., Whelan, R.J. & Auld, T.D., 2009. Characterizing the Litter in Postfire Environments: Implications for Seedling Recruitment. International Journal of Plant Sciences, 170(1), pp.53–60.

Eshel, A., Henig-Sever, N. & Ne'eman, G., 2000. Spatial variation of seedling distribution in an east Mediterranean pine woodland at the beginning of post-fire succession. Plant Ecology, 148(2), pp.175–182.

Facelli, J.M. & Pickett, S.T.A., 1991. Plant Litter : Its Dynamics and Effects on. Botanical Review, 57(1), pp.1–32.

Fernandes, P.M. et al., 2013. Prescribed burning in southern Europe: developing fire management in a dynamic landscape. Frontiers in Ecology and the Environment, 11(s1), pp.e4–e14.

Fernández, C., Vega, J. a & Fonturbel, T., 2013a. Fuel reduction at a Spanish heathland by prescribed fire and mechanical shredding: effects on seedling emergence. Journal of environmental management, 129, pp.621–7.

Fernández, C., Vega, J. a & Fonturbel, T., 2013b. Shrub resprouting response after fuel reduction treatments: comparison of prescribed burning, clearing and mastication. Journal of environmental management, 117, pp.235–41.

Fernández, C., Vega, J.A. & Fonturbel, T., 2013. Does fire severity influence shrub resprouting after spring prescribed burning? Acta Oecologica, 48, pp.30–36.

Fernández-Abascal, I., Tárrega, R. & Luis-Calabuig, E., 2004. Ten years of recovery after experimental fire in a heathland: effects of sowing native species. Forest Ecology and Management, 203(1-3), pp.147–156.

Ferrandis, P., Herranz, J.M. & MartinezSanchez, J.J., 1996. The role of soil seed bank in the early stages of plant recovery after fire in a Pinus pinaster forest in SE Spain. International Journal of Wildland Fire, 6(1), pp.31–35.

Ferrandis, P., Herranz, J.M. & Martinez-Sanchez, J.J., 1999. Fire impact on a maquis soil seed bank in Cabaneros National Park (central Spain). Israel Journal of Plant Sciences, 47(1), pp.17–26.

Fox, L.R. & Deveny, A.J., 2006. Indirect interactions between browsers and seed predators affect the seed bank dynamics of a chaparral shrub. Oecologia, 150(1), pp.69–77.

Gilbert, J.A. & Butt, K.R., 2010. Dispersal of Calluna vulgaris ( L .) Hull . seeds on severely burnt upland moorland. , 6(2000), pp.1–6.

Gross, K.L., 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology, 78(4), pp.1079–1093.

Hutchinson, T.F., Sutherland, E.K. & Yaussy, D.A., 2005. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. Forest Ecology and Management, 218(1-3), pp.210–228.

ICNF, 2013. Instituto da Conservação da Natureza e das Florestas. Available at: http://www.icnf.pt/portal/florestas.

Lopez, J., 2000. Production and morphology of fruit and seeds in Genisteae (Fabaceae) of south-west Spain. Botanical Journal of the Linnean Society, 132(2), pp.97–120.

Maia, P. et al., 2012. Fire severity as a key factor in post-fire regeneration of Pinus pinaster (Ait.) in Central Portugal. Annals of Forest Science, 69(4), pp.489–498.

Maia, P. et al., 2012. Wildfire effects on the soil seed bank of a maritime pine stand — The importance of fire severity. Geoderma, pp.1–9.

Moreira, B. et al., 2010. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. Annals of Botany, 105(4), pp.627–635.

Moreira, B., Tormo, J. & Pausas, J.G., 2012. To resprout or not to resprout: factors driving intraspecific variability in resprouting. Oikos, 121(10), pp.1577–1584.

Moreno, J.M., Oechel, W.C. & Dec, N., 2004. Fire Intensity Effects on Germination of Shrubs and Herbs in Southern California Chaparral SHRUBS AND HERBS IN SOUTHERN. , 72(6), pp.1993–2004.

Nathan, R. & Muller-landau, H.C., 2000. Spatial patterns of seed dispersal , their determinants and consequences for recruitment. Tree, 15(7), pp.278–285.

Ooi, M.K.J., Whelan, R.J. & Auld, T.D., 2006. Persistence of obligate-seeding species at the population scale: effects of fire intensity, fire patchiness and long fire-free intervals. International Journal of Wildland Fire, 15(2), pp.261–269.

Orscheg, C.K. & Enright, N.J., 2011. Patterns of seed longevity and dormancy in obligate seeding legumes of box-ironbark forests, south-eastern Australia. Austral Ecology, 36(2), pp.185–194.

Ottewell, K.M. et al., 2009. Genetic structure of seedling cohorts following repeated wildfires in the fire-sensitive shrub Persoonia mollis ssp nectens. Journal of Ecology, 97(4), pp.752–760.

Paula, S. & Pausas, J.G., 2008. Burning seeds: germinative response to heat treatments in relation to resprouting ability. Journal of Ecology, 96(3), pp.543–552.

Pérez, B. & Moreno, J.M., 1998. Methods for quantifying fire severity in shrubland-fires. Plant Ecology, 139, pp.91–101.

Podlussány, A., Jermy, T. & Szentesi, Á., 2001. On the leguminous host plants of seedpredator weevils (Coleoptera: Apionidae, Curculionidae) in Hungary. Acta Zoologica Academica Scientarium Hungaricae, 47(4), pp.285–299.

Prats, S.A. et al., 2012. Effectiveness of forest residue mulching in reducing post-fire runoff and erosion in a pine and a eucalypt plantation in north-central Portugal. Geoderma, 191, pp.115–124.

Prats, S.A. et al., 2013. Effectiveness of Hydromulching To Reduce Runoff and Erosion in a Recently Burnt Pine Plantation in Central Portugal. Land Degradation & Development, p.n/a–n/a.

Price, J.N. et al., 2010. Comparison of seedling emergence and seed extraction techniques for estimating the composition of soil seed banks. Methods in Ecology and Evolution, 1(2), pp.151–157.

Pyke, D. a., Brooks, M.L. & D'Antonio, C., 2010. Fire as a Restoration Tool: A Decision Framework for Predicting the Control or Enhancement of Plants Using Fire. Restoration Ecology, 18(3), pp.274–284.

Quintana, R. et al., 2004. Time of germination and establishment success after fire of three obligate seeders in a Mediterranean shrubland of central Spain. , pp.241–249.

Rego, F.C., Bunting, S.C. & Silva, J.M., 1991. Changes in understory vegetation following prescribed fire in maritime pine forests, 41(520), pp.21–31.

Rodriguez, E., Peco, B. & Gurrea, P., 2011. Effect of Scotch broom, Cytisus scoparius, pod size and patch density on Exapion fuscirostre (Coleoptera, Apionidae) seed weevil oviposition. Australian Entomological Society, 51(2), pp.127–132.

Silva, J. et al., 2009. Assessing the relative fire proneness of different forest types in Portugal. Plant Biosystems, 143(3), pp.597–608.

Thompson, K. & Band, S.R., 1997. Survival of a lowland heathland seed bank after a 33-year burial. Seed Science Research, 7(4), pp.409–411.

Trabaud, L., 1994. Diversity of the Soil Seed Bank of a Mediterranean Quercus-Ilex Forest. Biological Conservation, 69(1), pp.107–114.

Valbuena, L., Nuñez, R. & Calvo, L., 2001. The seed bank in Pinus stand regeneration in NW Spain after wildfire. , pp.22–31.

Valbuena, L. & Trabaud, L., 1995. Comparison between the Soil Seed Banks of a Burnt and an Unburnt Quercus-Pyrenaica Willd Forest. Vegetatio, 119(1), pp.81–90.

Valbuena, L. & Trabaud, L., 2001. Contribution of the soil seed bank to post-fire recovery of a heathland. Plant Ecology, 152(2), pp.175–183.

Valbuena, L. & Vera, M.L., 2002. The effects of thermal scarification and seed storage on germination of four heathland species. , pp.137–144.

Vasques, A. et al., 2012. Germination in five shrub species of Maritime pine understory—does seed provenance matter? Annals of Forest Science, 69(4), pp.499–507.

Vaughton, G., 1998. Soil seed bank dynamics in the rare obligate seeding shrub, Grevillea barklyana (Proteaceae). Australian Journal of Ecology, 23(4), pp.375–384.

**Chapter 5**

# Post-fire plant diversity and abundance in pine and eucalypt stands in Portugal: effects of biogeography, topography, forest type and post-fire management

## Chapter 5

## Post-fire plant diversity and abundance in pine and eucalypt stands in Portugal - effects of biogeography, topography, forest type and post-fire management

This chapter is published as:

Maia, P., Keizer, J., Vasques, A., Abrantes, N., Roxo, L., Fernandes, P., Ferreira, A., Moreira, F. (2014). Post-fire plant diversity and abundance in pine and eucalypt stands in Portugal: effects of biogeography, topography, forest type and post-fire management. Forest Ecology and Management.

### Abstract

This study concerned the mid-term regeneration of the woody understory vegetation of pure and mixed stands of *Pinus pinaster* Ait. and *Eucalyptus globulus* Labill. in northern and central Portugal following wildfires in 2005 and 2006. Pine and eucalypt stands are the most widespread and most fire-prone forest types in Portugal. The main aim was to investigate the importance of biogeography, topography, forest type and post-fire management operations in explaining the patterns in shrub diversity (species richness) and abundance (cover). To this end, 284 study sites in four distinct biogeographic regions were sampled 5 to 7 years following the last wildfire. At each site, the presence and cover of individual shrub species were estimated using 4 sub-plot of approximately 10 $m^2$ each. The entire data set was analyzed by means of GLM using a total of seven explanatory variables: biogeographic region, forest type, three types post-fire management operations (soil tillage, tree harvesting, and shrub clearance), and two topographic variables (slope angle and elevation). The GLM analysis was also done for the individual biogeographic regions.

Biogeographic region and slope steepness were key factors explaining shrub species richness, albeit the role of slope angle was possibly linked to the intensity of past land use.

Biogeographic region equally played a significant role in explaining the cover of all shrubs together as well as of the shrubs of Leguminosae and Cistaceae. All three types of post-fire management operations appeared to hamper the recovery of resprouters and Leguminosae, whereas just tree harvesting and shrub clearance (but not soil tillage) negatively affected the cover of seeder species. These impacts of post-fire management operation had a noticeable region-specific component, being more relevant in the less productive biogeographic regions.

Also the role of forest type depended strongly on biogeographic region. It was only significant in the South Mediterranean region, where pine plantations had a higher total shrub cover as well as higher covers of seeders and Cistaceae. Possibly, however, this significant role of forest type could be due to the lower incidence of shrub clearance in the pine stands.

*Keywords:* Planted forests; Pine; Eucalypt; Post-fire shrub regeneration; Species richness; Post-fire management

## 5.1. Introduction

Forests are of the utmost importance for mankind as they provide a vast number of ecosystem services such as regulation of water fluxes, protection against soil (fertility) losses and conservation of plant and animal biodiversity (EuropeanComission, 2010). According to the insurance hypothesis (Bengtsson et al., 2000; Folke et al., 1996), the present and future ecosystem services provided by forests (and other ecosystems) depend heavily on their biodiversity as their biodiversity is fundamental to an ecosystem's resistance and resilience against disturbances. A large number of plant

species is considered essential for the continued provision of services by ecosystems, even if these species appear to be partially redundant in terms of ecosystem functioning (Isbell et al., 2011). Ecosystem resilience is of particular relevance for fire-prone forests such as the planted pine and eucalypt forests studied here, including because fire frequency in Portugal is not expected to reduce substantially in the near future (Fernandes et al. 2013; Moreira et al. 2011). The understory vegetation of western Iberian eucalypt and pine stands deserve special mention for their key role in the ecosystem service of water flux regulation and erosion protection, especially during the early stages of the so-called window-of-disturbance (e.g. Fernandez et al. 2011; Prats et al. 2012, 2013) and with important implications for long-term land-use sustainability (e.g. Grigal 2000). Conservation of present and future biodiversity is also relevant from an economic point of view, as biodiversity constitutes an important aspect in forest certification schemes such as FSC (Forest Stewardship Council) and, thus, in valorization of forest products.

A variety of factors is likely to affect the cover and floristic composition of the understory vegetation in burned forest plantations. Biogeographic regions, which encompass climatic, edaphic and topographic conditions, constitute limits to the distribution ranges of native species (e.g. Abella & Covington 2006; Lobo et al. 2001). Also topographic factors have often been pointed out as key variables in explaining floristic patterns, albeit not in a consistent manner. For example, Pausas (1994) found that woody species richness was negatively correlated with elevation in high-elevation mountain ranges, while Lobo et al., (2001) found the opposite for the Iberian Peninsula. In the case of forests, the species richness of the understory has been associated to the predominant tree species of the overstory (Suckling et al., 2001). However, it is often unclear if the role of forest type is due to direct or indirect effects, resulting for example from competition by the tree species, alterations in abiotic conditions (e.g. pine needle cast) or differences in forestry practices (Cavard et al., 2011; Macdonald and Kurulok, 2007). Management operations carried out following wildfires can be a

major driver in the regeneration of the understory vegetation from the direct fire effects, both in terms of its cover and its species diversity (Vallejo and Alloza, 2012). A wide range of management operations have been applied in recently burnt areas, ranging from tree harvesting, to soil tillage in preparation of new plantations, to restauration actions such as seeding. All such operations can be expected to affect vegetation persistence and/or (re-)colonization following wildfires (Hartley, 2002).

Forests in Portugal, like in other parts of southern Europe, have changed profoundly over the past few decades, especially due the widespread planting of commercial tree species such as *Pinus pinaster* Ait. (for wood production) and eucalypt and, in particular, *Eucalyptus globulus* Labill. (for paper pulp production). At present, planted forests dominated by maritime pine and/or eucalypt constitute approximately 50 % of the forested area in Portugal (ICNF, 2013). Since the tree layer of these planted forests is composed of just one or two species, the understory vegetation largely determines these forests' plant species diversity. Bengtsson et al. (2000) considered the understory vegetation of mono-specific plantations as the best indicator of their overall biodiversity and, thereby, of their sustainability. An important drawback of pure and mixed stands of pine and eucalypt is their elevated flammability (Fernandes, 2009;Silva et al., 2009). To reduce their intrinsic fire hazard, pine and eucalypt plantations are typically subjected at regular intervals to reductions of the standing biomass of the understory vegetation, traditionally by grazing and shrub collection for livestock bedding and presently by mechanical shrub clearance and increasingly prescribed burning (e.g. Oliveira, 1999). These fuel management operations, however, can be expected to interfere with the biodiversity of the understory and, thus, with the principles of sustainable management.

The present study is a follow-up of Moreira et al (2014), which concerned the native and exotic tree species in pure and mixed stands of Maritime pine and eucalypt that had burnt 5-7 years earlier and which showed that biogeographic region and post-fire management operations were the most important factors explaining native tree species

diversity. This study, on the other hand, concerned the mid-term post-fire regeneration of the woody understory vegetation. The specific objectives of this study were: (i) to describe the patterns in shrub species richness as well as in their total cover and in the cover of the two main plant functional groups (in terms of fire adaptation strategy) and of the most common families; (ii) to explain these patterns in terms of potential explanatory variables related to biogeographic region, topography, forest type and post-fire management operations.

## 5.2. Materials and Methods

### 5.2.1. Study Area

Within northern and central Portugal, twenty study areas were selected that according to the Portuguese digital atlas of burnt areas had burnt in 2005 or 2006. The selection of these areas furthermore involved the following criteria: (i) the presence of sufficient numbers of mono-specific and/or mixed stands of eucalypt and maritime pine; (ii) the size of the burnt area (which ranged from 137 to 10,924 ha); (iii) accessibility. The number of pure and mixed eucalypt and pine stands was estimated using the data of the 5th National Forest Inventory (NFI) of 2005-2006 (ICNF, 2013). From the NFI grid points within each area that corresponded to pure and mixed eucalypt and pine stands, up to 30 were selected in a random stratified manner such that the study sites were equally divided over the three forest types as possible. The final selection of the study sites involved a field check in terms of accessibility, indications for the occurrence of a fire in 2005/2006 and the occurrence of a change in forest type following the NFI of 2005-2006, as further detailed in Moreira et al. (2013) and Águas et al. (2014). Sites that were recently planted or sites where the spontaneous vegetation was eliminated by recent forestry operations were not included in this study.

### 5.2.2. Field Sampling

A total of 284 study sites were sampled between the winter of 2010 and the late spring of 2012, by which time the sites had burnt for the last time between 5 and 7 years earlier. At each site, a sampling plot was laid out that consisted of a circular buffer with a radius of 6.78 m (**Figure 15**), using as center the coordinates of the respective NFI grid point. For this study, sampling itself was carried out in four sub-plots with a radius of 1.78 m, whose center was located at 5 m distance from the center of the plot in the four cardinal directions (N, E, S, W). Within each sub-plot, the woody species making part of the understory (further referred to as "shrub" species) were recorded and their projected aerial cover estimated visually. To this end, 12 cover classes were recognized: 0 %, >0 –5%, >5–10%, >10–20%, >20–30%, etc.

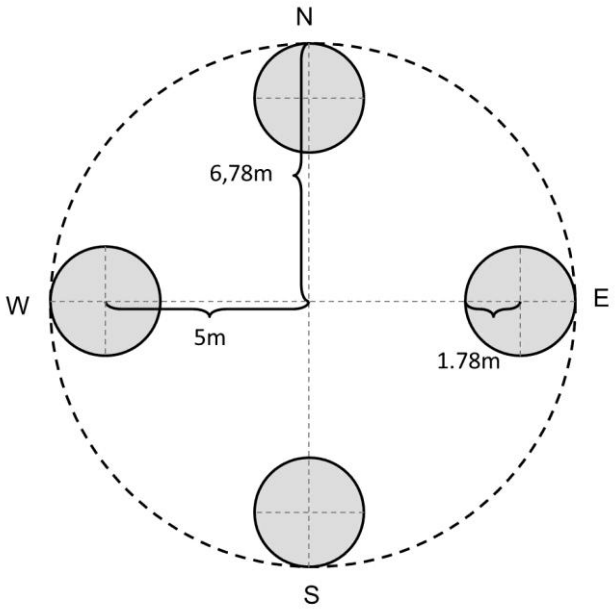



**Figure 15** - Schematic view of a sampling plot and its four sub-plots.

Evidence of forest management operations that had taken place after the wildfire of 2005/2006 was recorded based on direct observations and, whenever possible, complemented with information provided by land owners and/or forest managers. The following three types of management operations were recognized for their expected impact on the understory: (a) harvesting of burned trees; (b) soil tillage (including

harrowing, ploughing, and soil ripping); (c) cutting of the understory vegetation. Furthermore, the elevation and slope angle of the sampling plots were measured in the field.

### 5.2.3. Data analysis

This study analyzed the following response variables: (1) species richness (number of woody species); (2) total cover of the shrub species; (3) total cover of the shrub species classified as resprouters; (4) total cover of the shrub species classified as seeders); (5) cover of individual shrub families and, in particular, the Leguminosae, Cistaceae, and Ericaceae for occurring most frequently in the data set. The classification in seeders and resprouters was based on the species' post-fire regeneration strategies as reviewed by Paula and Pausas (2008) and Paula *et al*. (2009), including under resprouters both facultative and obligate resprouters (coded as S and R in Annex 1). In case a species' strategy was not specified in Paula and Pausas (2008) or in Paula *et al*. (2009), it was determined by observations during the field work.

The above-mentioned response variables were modeled by means of Generalized Linear Modeling (GLM), using IBM SPSS v.19 for Windows. In the case of species richness, this was done using a Poisson distribution with a log link, following Moreira et al (2013); in the case of the various cover variables, it involved a Tweedie distribution with a log link for providing the best fit in most instances.

A total of seven explanatory variables were considered for model selection in GLM. Organized by measurement scale, they were: (A) categorical variables: – (1) biogeographic region; 2) forest type (mono-specific eucalypt plantation; mono-specific Maritime pine plantation; mixed eucalypt-Maritime pine stand); (B) binomial variables, associated to post-fire management operations: (4) soil tillage; (5) tree harvesting; (6) shrub clearance; (C) continuous variables: (7) slope angle; (8) elevation. The

biogeographic region of the study sites was derived from the maps by Rivas-Martínez and Rivas-Saenz (1996-2009). The following four regions were used in this study:: (1) the Atlantic European Region, Cantabroatlantic Sub-region (hereafter “Atlantic”); (2) the Mediterranean Region, CoastalLusitano Andalusian Sub-region, Sado-Divisorian Province (hereafter “Coastal”): (3) the Mediterranean Western Iberian Sub-region, Carpetano Leonese Province (hereafter “North Mediterranean”); (4) the Mediterranean Western Iberian Sub-region, Luso-Extremadurense Province (hereafter “South Mediterranean”). As shown in **Figure 16**, however, the study sites that were located in the inland part of the Coastal-Lusitano Andalusian Sub-region (“Coastal”) were included here in the “South Med.” region (**Supplementary Material 2**). Model selection in GLM involved the stepwise backwards selection procedure, starting with all seven exploratory variables (Myers, 1990; Quinn and Keough, 2002). The percentage of deviance explained by each model was calculated as proportion of the deviance explained by the intercept-only model.

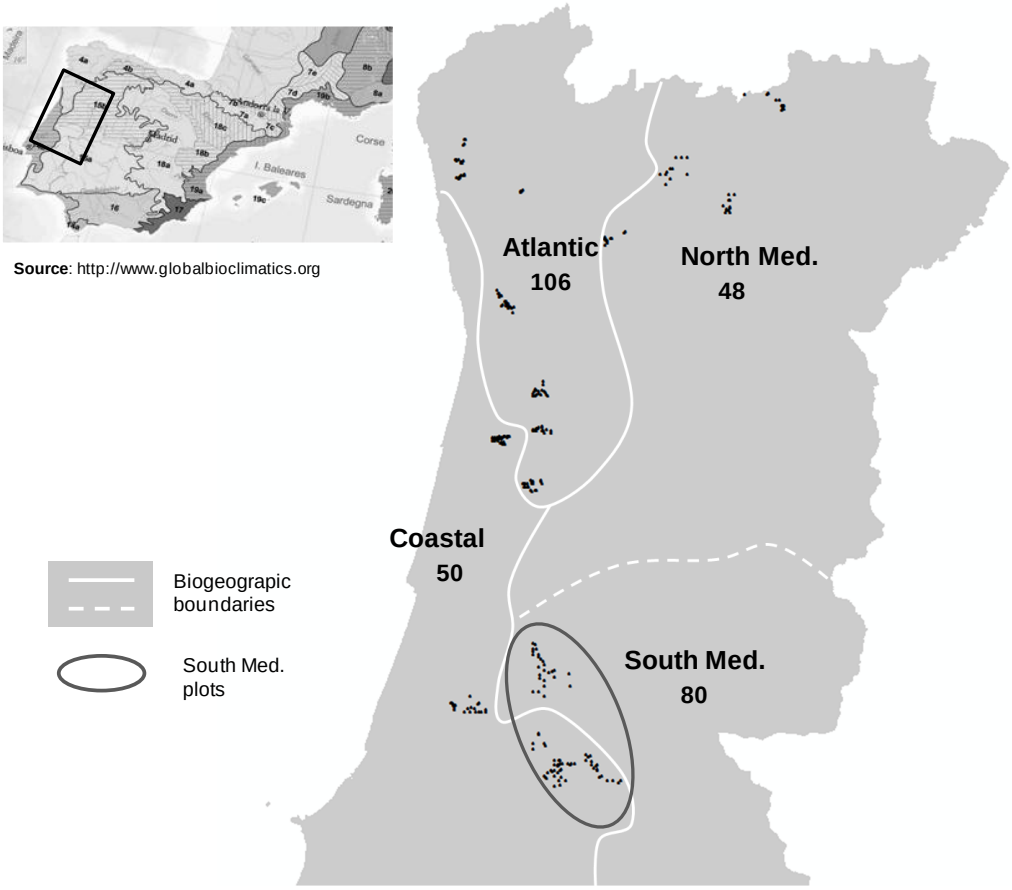



**Figure 16** - Biogeographic regions of study area. Dots in the main figure are sampling plots and sample numbers are indicated for each region. Upper left corner inset is an excerpt of the original cartography, for the Western Iberian Peninsula (www.globalclimatics.org). 4a – Atlantic European Region, Cantabroatlantic Subregion; 14 and 15 - – Mediterranean Region 14b –- Coastal– Lusitano Andalusian sub region, Sado-Divisorian province; 15 –- Mediterranean Western Iberian sub region; 15a - – Luso-Extremadurense province; 15b – Carpetano Leonese province. These designationscorrespond, respectively to the designations in the main figure: Atlantic, Coastal, South Mediterranean and North Mediterranean. The South Mediterranean region included the plots sampled in the Luso-Extremadurense province, and also the most inland plots of the Coastal-Lusitano Andalusian sub-region.

GLM was not only done for the entire data set but also for each of the four individual biogeographic regions separately to detect region-specific effects of forest type, management operations and topographic factors.

## 5.3. Results

### 5.3.1. Overall description of the data set

Roughly half of the sampling plots concerned mono-specific eucalypt plantations (46 %), whereas the rest of the plots was about evenly distributed over mono-specific Maritime pine plantations (30 %) and mixed eucalypt-pine stands (25 %) (**Table 8**). Almost 70 % of the sampling plots had undergone tree harvesting after the 2005/2006 fire, whilst similar amounts of plots had undergone either soil tillage (17 %) or shrub clearance (14 %).

Shrubs were encountered in almost all sampling plots (99 %) and had, on average, attained an elevated cover (87 %) over the 5 to 7 years after the last fire (Annex I). A total of 64 shrub species were found in the 284 sampled plots, with a mean species richness of 7 species per sampling plot. Resprouter species were present in basically all sampling plots (97 %), whilst seeder species occurred somewhat less frequently (81 %). However, the resprouters were clearly more abundant than the seeders, with a mean cover of 68 % as opposed to 32 %. The cover of the resprouters was by and large due to obligate resprouter species, as facultative resprouters were insignificant in terms of cover.

**Table 8** - Summary of the variables used in the analysis. Frequency (%) of forest type, management operations and mean and coefficient of variation of the topographic variables (slope and elevation) in each Biogeographic Region. Relative frequency of the plots sampled in each region is given in the first line of the Table. Frequency of post- fire management operations by forest type is given for the four biogeographic regions. pin –Pine plantations, euc – Eucalypt plantations, mix – mixed forests.

| | **frequency (%)** | | | | |
|---|---|---|---|---|---|
| | **Atlantic** | **Coastal** | **NorthMed** | **SouthMed** | **All regions** |
| | 37.3 | 17.6 | 16.9 | 28.2 | |
| **Forest Type** | | | | | |
| Pine | 17.9 | 10.0 | 72.9 | 31.3 | 29.6 |
| Eucalypt | 45.3 | 62.0 | 18.8 | 52.5 | 45.8 |
| Mixed | 36.8 | 28.0 | 8.3 | 16.3 | 24.6 |
| **Post-fire Management** | | | | | |
| **Soil tillage** | **19.8** | **32.0** | **12.5** | **6.3** | **16.9** |
| pin | 21.1 | 20.0 | 0.0 | 0.0 | |
| euc | 27.1 | 38.7 | 44.4 | 11.9 | |
| mix | 10.3 | 21.4 | 50.0 | 0.0 | |
| **Tree harvest** | **60.4** | **88.0** | **60.4** | **72.5** | **68.7** |
| pin | 57.9 | 100,0 | 57.1 | 68.0 | |
| euc | 54.2 | 83.9 | 66.7 | 76.2 | |
| mix | 69.2 | 92.9 | 75.0 | 69.2 | |
| **Shrub clearance** | **11.3** | **18.0** | **0.0** | **23.8** | **14.1** |
| pin | 15.8 | 20.0 | 0.0 | 8.0 | |
| euc | 8.3 | 9.7 | 0.0 | 38.1 | |
| mix | 12.8 | 35.7 | 0.0 | 7.7 | |
| *at least one operation* | *74.5* | *94.0* | *64.6* | *75.0* | *76.4* |

| **Topography** | **Mean (c.v.)** | | | |
|---|---|---|---|---|
| Slope(º) | 15.3(0.5) | 11.2(1.0) | 17.3 (0.4) | 17.8 (0.5) |
| Altitude (m) | 344.2(0.7) | 147.3(0.5) | 556.8(0.3) | 282.8(0.3) |

The three most frequent families in the data set were the Leguminosae (93 %), Ericaceae (80%) and Cistaceae (51 %) (**Supplementary Material 2**). In the same order, they were also the most abundant families, with a mean cover of 37, 28 and 13 %, respectively. The most common species of each of these three families were Pterospartum tridentatum (Leguminosae), *Calluna vulgaris* (Ericaceae) and *Cistus ladanifer* (Cistaceae). They were present in 48, 48 and 14 % of the sampling plots, respectively. Worth referring was the contrast in post-fire strategies among the three families. All shrub species pertaining to the Leguminosae family corresponded to resprouters (i.e. obligate or facultative resprouters), whereas all Cistaceae species were seeders. By contrast, the Ericaceae species included both resprouters and seeders.

### 5.3.2. Key factors explaining shrub species richness and shrub cover

The shrub species richness could be explained to a significant extent by biogeographic region and slope angle, with the resulting GLM accounting for 23 % of the total variation (**Table 8**). The role of biogeographic region reflected clear differences in mean shrub species richness, ranging from 9 in the Coastal and South Mediterranean regions to 7 in the Atlantic region (**Supplementary Material 2**) and 5 in the North Mediterranean region. The role of slope angle corresponded to a tendency for the number of shrub species to increase with increasing with slope steepness.

**Table 9** - Generalized Linear Models for each of the response variables: richness of Woody species in the understory layer and plant cover variables. P values of the model (partial or omnibus) are given with asterisks - p<0.05( *) - p<0.01(**) - p<< 0.01(***); + and – signs indicate significant differences (between Biogeographic region, Forest Type) or significant correlation sign (slope or elevation); for the Post-fire management it indicates significant differences between plots with and without evidences of the specific management operation.

| Variables | Shrub Species Richness | Cover | | | | | |
|---|---|---|---|---|---|---|---|
| | | Total Shrub | Post-fire regeneration | | Families | | |
| | | | Resprouters | Seeders | Leguminosae | Cistaceae | Ericaceae |
| **Biogeographic Region** | *** | *** | ** | *** | *** | *** | n.s. |
| **Atlantic** | + | | + | + | + | | |
| **Coastal** | ++ | + | + | + | + | | |
| **NorthMed** | | | | | | + | |
| **SouthMed** | ++ | + | + | ++ | + | + | |
| **Forest type** | n.s. | n.s. | n.s. | n.s. | n.s. | * | n.s. |
| **Pine** | | | | | | + | |
| **Euc** | | | | | | | |
| **Mix** | | | | | | | |
| **Post-Fire Management** | n.s. | | | | | n.s. | n.s. |
| **Soil tillage** | | *** (-) | ** (-) | n.s. | * (-) | | |
| **Tree harv** | | ** (-) | ** (-) | n.s. | * (-) | | |
| **Shrub clear** | | *** (-) | ** (-) | ** (-) | ** (-) | | |
| **Topography** | | | | | n.s. | n.s. | n.s. |
| **Slope angle** | * (+) | | | | | | |
| **Elevation** | | ** (-) | **(-) | ~* (-) | | | |
| **Omnibus test p** | *** | *** | *** | *** | *** | *** | n.s. |
| **% VarianceExplained** | 26.2 | 23.2 | 17.2 | 22.8 | 15.6 | 19.9 | - |

The total shrub cover was explained best by a GLM that included biogeographic region, post-fire management and elevation as significant factors. Together, these three factors explained 23 of the variation. The importance of biogeographic region was due to a marked contrast in total shrub cover between the North Mediterranean region (60 %), on the one hand, and, on the other, the Coastal and South Mediterranean regions (95 and 113 %, respectively), The role of post-fire management reflected a negative impact of all three management types on total shrub cover, while the effect of elevation corresponded to a decrease in total shrub cover with increasing elevation.

The best GLMs for the resprouter as well as seeder cover closely resembled that for the total shrub cover, as they involved the same three significant explanatory variables and accounted for comparable fractions of the total variation (17 and 23 %,

respectively). Furthermore, also resprouter and seeder cover were clearly lower in the North Mediterranean region than in the other regions (43 vs. 69-84 % and 8 vs. 28-49 %). Nonetheless, the biogeographical pattern in seeder cover differed from that in resprouter cover (and that in total shrub cover) in that its mean cover was highest in the Coastal region instead of in the South-Mediterranean region. The seeder cover also revealed a distinct response to post-fire management than the respouter cover (and the total shrub cover). While the resprouter cover, like the total shrub cover, was negatively affected by all three types of management operations, the seeder cover was not significantly impacted by either soil tillage or tree harvesting).

The GLM results differed notably between the three most common families. In the case of the Ericaceae, none of the seven explanatory variables could account for a significant fraction of the cover variation. The best GLM for the Leguminosae cover was similar to that for the resprouter cover, as the different biographic regions and the three post-fire management operations had analogous significant effects and as the explained variance was almost identical (16%). The best GLM for the Cistaceae cover, however, was the only one in the present study that included forest type as significant factor. This role of forest type coincided with a higher Cistaceae cover in mono-specific Maritime pine plantations than in mono-specific eucalypt plantations or mixed eucalypt-pin stands. The Cistaceae cover further stood out amongst the different covers analyzed here (including that of Ericaceae) in that its mean value was not clearly lowest in the North Mediterranean region.

### 5.3.3. Key factors for the individual biogeographic regions

The significant role of slope angle in explaining shrub species richness in the entire data set appeared to be highly region-specific (**Table 10**). In fact, the general pattern of increasing richness with increasing slope angle was only verified for the South

Mediterranean region. This region combined relatively steep slopes of, on average, 17.8 º (**Table 8**) with a comparatively high shrub species richness of, on average, 9 species (**Supplementary Material 2**). The species suit of the South Mediterranean region furthermore included a comparatively large number of characteristic species, i.e. species that occurred clearly more frequently in one region than in the other three regions (10 vs. 2-5). From the ten characteristic *taxa* of the South Mediterranean region, the following four were almost exclusively found there: *Cistus monspeliensis*, *Ulex airensis*, *Ulex jussiaei* and *Lavandula* spp..

**Table 10** - Generalized Linear Models for the effects of Forest Type, Post-Fire management and Topography, for the individual Biogeographic regions. The Biogeographic regions for which the explanatory variables (rows) are significant in explaining the variability of the response variables (columns) are indicated as follows: Atl (Atlantic), Nmed (North Mediterranean), Smed (South Mediterranean). P values of the effect are given with asterisks, following the abbreviation of the Biogeographic Region where the effect is statistically significant. p<0.05( *) - p<0.01(**) - p< 0.001(***). + and – signs indicate significant differences between plots with and without evidences of the specific management operation or significant correlation sign (slope or elevation).

| Variables | Woody Species Richness | % Cover | | | | |
|---|---|---|---|---|---|---|
| | | Total Shrub | Post-fire regeneration | | Families | |
| | | | Resprouters | Seeders | Leguminosae | Cistaceae |
| **Forest type** | | Smed * | | Smed* | | Smed ** |
| **Pine** | | + | | + | | + |
| **Euc** | | - | | | | - |
| **Mix** | | | | | | |
| **Post-fire Management** | | | | | | |
| **Soil tilling** | | Atl (-) **<br>Nmed(-)** | Atl (-) ***<br>Nmed(-) * | | Atl (-) ** | Coast (-)** |
| **Tree harvest** | | Nmed(-)* | Atl (-) ** | Nmed (-)*<br>Smed (-)* | | |
| **Shrub clear** | Smed (-) * | Atl (-) **<br>Smed (-) *** | Atl (-) **<br>Smed (-) * | Smed (-) ** | Atl (-) **<br>Smed (-) ** | |
| **Topography** | | | | | | |
| **Slope** | Smed (+) *** | Smed (+) ** | | Nmed (-)* | | |
| **Elevation** | | Nmed (-) ** | Atl (-) *<br>Coast (-) *<br>Nmed(-) * | Smed (-) * | Nmed (-) * | Smed (-)** |
| **% VarianceExplained** | | | | | | |
| **Atl** | - | 12.5 | 24.5 | - | 11.5 | - |
| **Coast** | - | - | 8.8 | - | - | - |
| **Nmed** | - | 25.3 | 12.7 | 15.9 | 7.3 | - |
| **Smed** | 21.4 | 28.8 | 11.7 | 21.2 | 9.3 | 11.6 |

Also in the case of the second topographic factor, elevation, there were clear discrepancies between its relevance in the entire data set and its importance in the individual biogeographic regions. The significant decrease in both total shrub cover and resprouter cover with increasing elevation was found for only one out of four biogeographic regions. By contrast, this same elevation-cover relationship was significant for the resprouters in three of the regions,

The various GLMs for the individual biogeographic regions equally revealed that the relevance of all three types of post fire management operations was markedly region-specific, since none of the significant management-cover relationships in the entire data set applied to more than two out of four regions. Even so, soil tillage and shrub clearance tended to have a more widespread impact than tree harvesting, playing a significant role in two regions instead of one. While soil tillage was especially relevant in the Atlantic and North Mediterranean regions, shrub clearance was particularly important in the Atlantic and South Mediterranean regions, both types of operations producing significant reductions in total shrub cover, resprouter cover and Leguminosae cover. Shrub clearance also diminished the seeder cover in the South Mediterranean region in a significant manner. Among these three regions, the North Mediterranean region stood out for its clearly lower mean values of total shrub, resprouter and Leguminosae cover; in turn, the South Mediterranean region had similar mean resprouter and Leguminosae covers than the Atlantic regions but a noticeably higher mean total shrub cover (113 % vs. 76 %). Worth noting, however, was that shrub clearance was not observed at any of the 48 study sites in the North Mediterranean region. Furthermore, the Coastal region deserved special mention for the exceptional lack of impact of post-fire management on its shrub cover, except in the case of the Cistaceae cover. At the same time, however, post-fire management was more frequent in the Coastal region than in any of the other three regions, with 94 % as opposed to 65-75 % of the study sites having been subjected to one or more types of

management operations. In spite of these frequent operations, the Coastal region had the highest resprouter cover of all four biogeographic regions (84 % vs. 43-73 %).

Forest type was of greater relevance in the region-specific GLM's than in the overall GLM's, playing a significant role not just in case of the Cistaceae cover but also in the case of the total shrub cover and of the seeder cover. Nonetheless, the statistical significance of forest type was restricted to a single biogeographic region, the South Mediterranean one. The mono-specific Maritime pine plantations had a positive effect on all three cover categories in the region, while the mono-specific eucalypt plantations had a negative effect on total shrub cover and Cistaceae cover but not on seeder cover. These effects were well-illustrated by the mean values of total shrub cover (pine: 142 %; euc: 71 %), seeders (pine: 71 %; euc&mix: 37-50 %) and Cistaceae (pine: 37 %; euc: 13 %).

## 5.4. Discussion

### 5.4.1. Factors affecting shrub species richness

The shrub species richness of mono-specific and mixed stands of Maritime pine and eucalypt in northern and central Portugal was significantly influenced by biogeographic region. The important role of biogeographic units in biodiversity patterns was also pointed out by previous studies (e.g. Moreira et al. 2013; Ihaddaden et al. 2013). Mean shrub species richness was highest in the Coastal and South Mediterranean regions, but the regions' identical figures could well have different origins. The high diversity in the Coastal region could be due to reduced inter-specific competition, reflecting the region's mild temperatures and elevated rainfall and, thus, limited water stress. By contrast, the high diversity in the South Mediterranean could be due to habitat diversity, reflecting the region's irregular topography as indicated by its relatively steep slopes (Lobo et al., 2001; Wohlgemuth, 1998).

The mean values of shrub species richness presented here were much lower than the richness figures of prior studies in the Iberian Peninsula and surrounding Mediterranean regions (Ihaddaden et al., 2013; Lobo et al., 2001; Pausas and Carreras, 1995). This could be due to the reduced size of the area sampled in each plot (approximately 40 m2), especially since species richness assessment typically depends strongly on spatial scale (Vetaas and Ferrer-Castán, 2008). This methodological aspect was also supported by the fact that the present figures of shrub species richness per biogeographic region were comparable to those of the study by Santana et al. (2011) on cork oak forests in Portugal.

Biogeographic Region was also found to be a key factor in determining woody species composition. The specific composition revealed a clear pattern, which followed the species ecological range (SPB, 2012-2013). For example, Erica arborea and Ulex europaeus were more frequent in the Atlantic region, while the South Mediterranean sites were comparatively more represented by species typical of Mediterranean communities, like Lavandula spp., Ulex airensis, Halimium ocymoides, Cistus monspeliensis and Cistus ladanifer (Annex 1).

The shrub species richness in this study also depended significantly on slope angle, both in the entire data set and in the South Mediterranean region. A significant relationship between slope angle and woody plant species was also found by Sharma et al. (2009) but it was opposite to that found here, with tree species richness decreasing with increasing slope angle. Sharma et al. (2009) interpreted their results as reflecting a decrease in establishment potential of the tree species on steeper slopes. Possibly, in the present case the role of slope angle was indirect, as a key factor shaping land-use intensity (Lobo et al. 2001). In the past, land use would have been less intensive on the steeper slopes, as the slopes' difficult access implied greater efforts and as their productivity was more marginal (Porto, Correia, and Beja 2011; Santana et al. 2011). Even in recent times as studied here, soil tillage – typically the most costly management option - was less frequent on the steeper slopes.

Possibly, however, the role of slope angle in this study reflected past rather than recent land-use patterns, since post-fire soil tillage was not found to have a significant influence on shrub species richness. The shrub species richness in the pure and mixed pine and eucalypt stands studied here was not significantly related to forest type. Likewise, the richness in native tree species in the same data set could not be explained to a significant extent by forest type (Moreira et al., 2013). These results would seem to go against the findings by Brockerhoff et al. (2008), whose review indicated that species richness would typically be higher in native forest than in exotic plantations. A possible explanation would be that not only the mixed and pure eucalypt stands but also the pure pine stands were planted forests and, thus, must have undergone considerable human intervention during the past century. Especially in the case of the mixed and pure pine stands, past human disturbance could have included regular thinning, shrub removal (e.g. as stable material) and grazing activities. In terms of management operations following the 2005/2006 fires, however, no obvious differences were found between the three forest types studied here. This lack of differences could, at least in part, be an artifact resulting from the decision to exclude the study sites that had recently suffered major impacts of management operations (see section 2.2).

### 5.4.2. Factors influencing shrub cover

The cover of (part of) the woody understory vegetation 5-7 years after the latest wildfire was found here to vary significantly with biogeographic region as well as with topographic factors and with the type of post-fire management operations. Apparently, while biogeographic setting in combination with topographic conditions defined the potential for post-fire re-covery of the shrub species, their two principal regeneration strategies and two of their most common families (i.e. Leguminosae and Cistaceae but not Ericaceae), post-fire management options determined the extent to which this

potential was achieved. From the two topographic factors considered in this study, elevation had a more consistent and widespread impact on shrub cover than slope angle, which contrasted with the factors' impacts on shrub species diversity. The decline in total or partial shrub cover in this study agreed well with the decrease in forest understory cover with elevation reported by Coll et al. (2010).

There was a marked contrast in the relevance of post-fire land management for the cover of the seeders than for the cover of the resprouters, especially in the entire data set. Seeder cover was hampered in a significant manner by shrub clearance and, in two out of four biogeographic regions, tree harvesting but not by soil tillage. Resprouter cover, however, was affected significantly by all three types of post-fire management operations. This differential effect of soil tillage on the cover of resprouters (as well as the Leguminosae family) could well be longer lasting than the period of 5-7 years following fire studied here, as soil tillage would easily produce major damage to the root systems of the resprouter plants and, thereby, seriously interfere with their capacity to recover from the damage by the fire and their resilience to possible adverse post-fire conditions. In the case of the obligate resprouter species, an aggravating factor is their typically low dispersal rate and, thus, reduced potential for re-colonization (e.g. Pausas and Vallejo 1999). In the case of the seeder species, the lack of relevance of soil tillage 5-7 years after the last fire fitted in well with their preferential allocation of resources to seed production and, hence, with their elevated capacity to regenerate from the soil seed bank and/or from external seed sources (e.g. Verdú 2000; Pausas and Paula 2011).

Although the above-mentioned differential impacts of three types of management operations made much sense, two aspects of the present data set deserve special mention as they might have contributed to an underrating of the role of soil tillage and, at the same time, to an overrating of the importance of tree harvesting and shrub clearance. In the first place, sites that had been recently been subjected to soil tillage were excluded from study, whereas sites that had recently undergone tree logging or

shrub clearance were not. In the second place, for the majority of study sites that had been tilled less recently it was it difficult to estimate when this soil tillage had taken place. Therefore, the present analyses could very well have included sampling plots that had been tilled before the 2005/2006 fire and, consequently, where especially resprouter species would have had more time to regenerate following soil tillage and before the fire.

Forest type also was a limited relevance for the shrub cover, except in the case of the South Mediterranean region where total shrub cover, seeder cover and Cistaceae cover were, on average, higher in mono-specific Maritime pine plantations than in pure or mixed stands of eucalypt. The effects of forest type on total shrub cover and seeder cover, however, could be indirect and be associated to impacts of post-fire management. Namely, shrub clearance was more frequent in the eucalypt stands of the South Mediterranean region than in those of the other regions, and shrub clearance was found to negatively affect both total shrub and seeder cover in the South Mediterranean region. In the case of the Cistaceae cover, the significant relation with forest type found could reflect competition (or other interactions) with the pine and eucalypt trees or differences in land-use history of the pine and eucalypt plantations prior to the 2005/2006 fires. The former explanation is perhaps less likely, as similar impacts would have been expected for the other native plant groups (see Chu et al. 2014). The latter explanation could involve repeated grazing and/or shrub clearing, leading to progressive impoverishment of the soil seed bank and, thus, the regeneration potential of Cistaceae species.

The Ericaceae family stood out for the lack of significant relations with any of the seven explanatory variables included in this study, not even with biogeographic region This could be due to the broad distribution range of this family throughout the Portuguese territory (SPB, 2012-2013). Another explanation could be that the Ericaceae species encountered in this study included both seeders and resprouters, unlike the Leguminosae species (all resprouters) or the Cistaceae species (all seeders). Possibly,

separate analysis of the resprouter and seeder species of Ericaceae would have yielded similar results as presented here for all resprouter/seeder species together, shedding further light on variability in vulnerability to disturbance regimes within the same family. Since this family is composed by post-fire seeders and resprouters (Annex 1) (Paula and Pausas, 2008), it may also explain why Ericaceae cover was unrelated with post-fire management operations –resprouters species, like Arbutus unedo and Erica australis, would be negatively affected by all management operations, but obligate seeders, like Calluna vulgaris or Erica umbellata, might not be significantly affected by soil tillage. A further step would be to repeat the GLM analyses for individual species (those occurring frequently enough in the data set). Especially a better understanding of management -impacts would seem of interest for the protection of specific taxa and, thereby, for increasing the value of mono-specific and mixed eucalypt and pine plantations, namely by adding to their biological value (Sharma and Henriques, 2005), by increasing their potential for forest conversion into native forests (Moreira et al., 2013), and by diversification of forest products (FSC 2012).

### 5.4.5. Management implications and further research

While this study did not address the effect of management operations on the growth of the main tree species, it showed clearly that management operations had negative impacts on the understory communities of pure and mixed pine and eucalypt plantations. Future research should focus in the analysis of the efficacy of typical management operations for attaining certain management goals. For example, cases of fertilization for eucalypt growth (e.g. Madeira, Fabião, and Carneiro 2011) or harrowing for eliminating competition and increase tree growth (e.g. Carneiro et al. 2008) did not lead to the expected outcome, but have hampered spontaneous vegetation structure and diversity. In other situations, mechanical soil preparation has increased the survival rates and growth of planted tree seedlings (Prévosto et al.,

2012), but on the contrary did decrease the diversity of trees (Prévosto et al., 2011), like Moreira et al. (2013) also verified.

Conservationist (biodiversity, resilience, provision of ecosystem services) and productivity (economic income: timber production, pay per services, forest certification) perspectives can co-exist in a sustainable forestry scheme (Bullock et al., 2011; Maes et al., 2012). A possibility is to designate areas exclusively for forest conservation, in the forest matrix (Bengtsson et al., 2000; Fischer et al., 2006), which is moreover, one of the requisites for the attribution of forest certification labels (principle 6 -FSC 2012). As this study suggests, such areas could be the steepest slopes, where 1) species richness is higher, 2) management operations are more expensive and less likely to produce high economic revenue, while 3) being potentially more damaging, namely by leading to high soil erosion rates (see Martins et al. 2013).

### 5.5. Conclusions

The main conclusions of this study into the woody understory vegetation of Maritime pine and eucalypt in northern and central Portugal that had burnt five to seven years earlier by wildfires were as follows:

**1.** Shrub species richness could be explained to a significant extent by biogeographic region and slope angle but not by post-fire management operations (soil tillage, tree logging, shrub clearance) or by forest type. The - unexpected - increase in shrub species richness with increasing slope steepness was possibly due to less intense land use on steeper slopes, especially in the period before the last wildfires, than to differences in ecological conditions per se.

**2.** Total shrub cover was significantly related to biogeographic region and, at the same time, notably hampered by management operations after the last fire.

**3.** The covers of seeders and resprouters contrasted sharply in their response to post-fire management operations in that resprouter cover was significantly affected by all

three types of operations, while seeder cover was significantly affected by tree harvesting as well as shrub clearance but not by soil tillage.

**4.** The negative impacts of post-fire management operations on shrub cover typically had a strong region-specific component, with the impacts being more pronounced in the less productive biogeographic regions with their more marginal ecological conditions.

**Acknowledgements**

This study was supported by the FCT in the framework of the project "FIREREG - Factores que determinam a variabilidade da regeneração pós-fogo em Pinus pinaster e Eucalyptus globulus em Portugal: implicações para a biodiversidade e gestão pós-incêndios" - (PTDC/AGR-CFL/099420/2008), as well as individual research grants attributed to P. Maia (SFRH/ BD/42168/2007), A. Vasques (SFRH/B/47522/2008) and N. Abrantes (SFRH/BPD/84833/2012). The authors want to thank Mariana Pedro, Inês Camarinha, Ana Lima, Bart van der Slik, Irina Oliveira, Ana Águas, Lia Tânia-Diniz for their important help with the field sampling. Paulo Silveira and Rosa Pinho are gratefully acknowledged for their help in the identification of "difficult" species. The authors further wish to acknowledge the contribution of Mariana Pedro in preliminary analyses. The authors are further grateful to the people of the forest associations AFLOMAÇÃO and "Associação Florestal do Baixo Vouga", who.provided vital information on post-fire management at the study sites. Finally, the authors want to thank two anonymous referees for their comments, which allowed to markedly increase the quality of this manuscript.

**References**

Abella, S.R. & Covington, W.W., 2006. Vegetation–environment relationships and ecological species groups of an Arizona Pinus ponderosa landscape, USA. Plant Ecology, 185(2), pp.255–268.

Águas, A. et al., 2014. Natural establishment of Eucalyptus globulus Labill. in burnt stands in Portugal. Forest Ecology and Management, 323, pp.47–56.

Bengtsson, J. et al., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management, 132(1), pp.39–50.

Bullock, J.M. et al., 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends in ecology & evolution, 26(10), pp.541–9.

Carneiro, M. et al., 2008. Effects of harrowing and fertilisation on understory vegetation and timber production of a Eucalyptus globulus Labill. plantation in Central Portugal. Forest Ecology and Management, 255(3-4), pp.591–597.

Cavard, X. et al., 2011. Importance of mixedwoods for biodiversity conservation : Evidence for understory plants , songbirds , soil fauna , and ectomycorrhizae in northern forests. , 161, pp.142–161.

Chu, C. et al., 2014. Allelopathic effects of Eucalyptus on native and introduced tree species. Forest Ecology and Management.

Coll, L. et al., 2010. Predicting understory maximum shrubs cover using altitude and overstory basal area in different Mediterranean forests. European Journal of Forest Research, 130(1), pp.55–65.

EuropeanComission, 2010. GREEN PAPER On Forest Protection and Information in the EU: Preparing forests for climate change (COM(2010)66 final), Available at: http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=COM:2010:0066:FIN:EN:PDF.

Fernandes, P., 2009. Combining forest structure data and fuel modelling to classify fire hazard in Portugal. Annals of Forest Science, 66(4), p.415.

Fernandes, P.M. et al., 2013. Prescribed burning in southern Europe: developing fire management in a dynamic landscape. Frontiers in Ecology and the Environment, 11(s1), pp.e4–e14.

Fernandez, C. et al., 2011. Effectiveness of three post-fire treatments at reducing soil erosion in Galicia (NW Spain). International Journal of Wildland Fire, 20(1), pp.104–114.

Fischer, J., Lindenmayer, D.B. & Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment, 4(2), pp.80–86.

Folke, C., Holling, C.S., Perrings, C., 1996. Biological diversity, ecosystems, and the human scale. Ecol. Appl., 6, pp.1018-1024.

Forest, C.F.O.R., 2012. Forest Stewardship Council - FSC Principles and Criteria fos Forest Stewardship.

Grigal, D.F., 2000. Effects of extensive forest management on soil productivity, For.Ecol.Manage., 138, pp.167-185.

Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology and Management, 155(1-3), pp.81–95.

ICNF, 2013. Instituto da Conservação da Natureza e das Florestas. Available at: http://www.icnf.pt/portal/florestas.

Ihaddaden, A. et al., 2013. Climate and vegetation structure determine plant diversity in Quercus ilex woodlands along an aridity and human-use gradient in Northern Algeria. Flora, 208(4), pp.233–298.

Isbell, F. et al., 2011. High plant diversity is needed to maintain ecosystem services. Nature, 477(7363), pp.199–202.

Lobo, J.M., Castro, I. & Moreno, J.C., 2001. Spatial and environmental determinants of vascular plant species richness distribution in the Iberian Peninsula and Balearic Islands. Biological Journal of the Linnean Society, 73(2), pp.233–253.

Macdonald, S.E. & Kurulok, S.E., 2007. Impacts of postfire salvage logging on understory plant communities of the boreal mixedwood forest 2 and 34 years after disturbance. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 37(12), pp.2637–2651.

Madeira, M., Fabião, A. & Carneiro, M., 2011. Do harrowing and fertilisation at middle rotation improve tree growth and site quality in Eucalyptus globulus Labill. plantations

in Mediterranean conditions? European Journal of Forest Research, 131(3), pp.583–596.

Maes, J. et al., 2012. Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. Biological Conservation, 155, pp.1–12.

Martins, M. a. S. et al., 2013. Runoff and inter-rill erosion in a Maritime pine and a Eucalypt plantation following wildfire and terracing in north-central Portugal. Journal of Hydrology and Hydromechanics, 61(4), pp.261–268.

Moreira, F. et al., 2011. Landscape - wildfire interactions in southern Europe: Implications for landscape management. Journal of Environmental Management, 92(10), pp.2389–2402.

Moreira, F. et al., 2013. Occurrence of native and exotic invasive trees in burned pine and eucalypt plantations: Implications for post-fire forest conversion. Ecological Engineering, 58, pp.296–302.

Myers, R.H., 1990. Classical and Modern Regression with Applications, Duxbury Classic Series.

Oliveira, A., 1999. Boas Práticas Florestais para o Pinheiro Bravo. Centro Pinus - Associação para a Valorização da Floresta.

Paula, S. et al., 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology, 90(5).

Paula, S. & Pausas, J.G., 2008. Burning seeds: germinative response to heat treatments in relation to resprouting ability. Journal of Ecology, 96(3), pp.543–552.

Pausas, J.G., 1994. Species Richness Patterns in the Understorey of Pyrenean Pinus-Sylvestris Forest. Journal of Vegetation Science, 5(4), pp.517–524.

Pausas, J.G. & Carreras, J., 1995. The Effect of Bedrock Type, Temperature and Moisture on Species Richness of Pyrenean Scots Pine (Pinus-Sylvestris L) Forests. Vegetatio, 116(1), pp.85–92.

Pausas, J.G. & Paula, S., 2011. Root traits explain different foraging strategies between resprouting life histories. Oecologia, 165(2), pp.321–331.

Pausas, J.G., Vallejo, R., 1999. The role of fire in European Mediterranean Ecosystems. In: Chuvieco, E. (Ed.), Remote Sensing of Large Wildfires in the European Mediterranean Basin. Springer, Verlag, pp 3-16.

Porto, M., Correia, O. & Beja, P., 2011. Long-term consequences of mechanical fuel management for the conservation of Mediterranean forest herb communities. Biodiversity and Conservation, 20(12), pp.2669–2691.

Prats, S.A., MacDonald, L.H., Monteiro, M., Ferreira, A.J.D., Coelho, C.O.A., Keizer, J.J.,2012. Effectiveness of forest residue mulching in reducing post-fire runoff and erosion in a pine and a eucalypt plantation in north-central Portugal. Geoderma 191, 115–125.

Prats, S.A. et al., 2013. Effectiveness of Hydromulching To Reduce Runoff and Erosion in a Recently Burnt Pine Plantation in Central Portugal. Land Degradation & Development, p.n/a–n/a.

Prévosto, B. et al., 2011. Effects of different site preparation treatments on species diversity, composition, and plant traits in Pinus halepensis woodlands. Plant ecology, 212(4), pp.627–638.

Prévosto, B. et al., 2012. Regenerating mature Aleppo pine stands in fire-free conditions : Site preparation treatments matter. Forest Ecology and Management, 282, pp.70–77.

Quinn, G.P. & Keough, M.J., 2002. Experimental design abd data analysis for biologists, Cambridge University Press.

Rivas-Martínez, S., Worldwide Bioclimatic Classification System, Available at: http://www.globalbioclimatics.org/form/maps.htm.

Santana, J. et al., 2011. Long-term understory recovery after mechanical fuel reduction in Mediterranean cork oak forests. Forest Ecology and Management, 261(3), pp.447–459.

Sharma, S. & Henriques, I., 2005. Stakeholder influences on sustainability practices in the Canadian forest products industry. Strategic Management Journal, 26(2), pp.159–180.

Sharma, C.M., Suyal, S., Gairola, S., Ghildiyal, S.K., 2009. Species richness and diversity along an altitudinal gradient in moist temperate forest of Garhwal

Himalaya. J. Am. Sci. 5, 119–128.

Silva, J. et al., 2009. Assessing the relative fire proneness of different forest types in Portugal. Plant Biosystems, 143(3), pp.597–608.

Sociedade Portuguesa de Botânica, Flora-on - Flora de Portugal interactiva. Available at: http://www.flora-on.pt/.

Suckling, D.M. et al., 2001. Behavioral and electrophysiological responses of Arhopalus tristis to burnt pine and other stimuli. Journal of Chemical Ecology, 27(6), pp.1091–1104.

Vallejo, V.R. & Alloza, J.A., 2012. Post-Fire Management in the Mediterranean Basin. Israel Journal of Ecology & Evolution, 58, pp.251–264.

Verdú, M., 2000. Ecological and evolutionary differences between Mediterranean seeders and resprouters. , 11, pp.265–268.

Vetaas, O.R. & Ferrer-Castán, D., 2008. Patterns of woody plant species richness in the Iberian Peninsula: environmental range and spatial scale. Journal of Biogeography, 35(10), pp.1863–1878.

Wohlgemuth, T., 1998. Modelling floristic species richness on a regional scale: a case study in Switzerland. Biodiversity & Conservation, 7(2), pp.159–177.

## Supplementary Material

**Supplementary Material 2** - Floristic composition by Biogeographic Region.

| | | | | | Mediterranean | | | | | | overall | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Atlantic | | Coastal | | North Med. | | South Med. | | | |
| | | N | 106 | | 50 | | 48 | | 80 | | 284 | |
| **Family** | **Species** | **Reg** | freq. % | mean cover% | freq. % | mean cover% | freq. % | mean cover% | freq. % | mean cover% | freq. % | mean cover% |
| LEG | Leguminosae | R | 97 | 37.0 | 100 | 47.3 | 75 | 18.6 | 76 | 41.4 | 93 | 36.9 |
| ERI | Ericacea | R/S | 83 | 27.5 | 94 | 37.9 | 56 | 20.9 | 66 | 28.3 | 80 | 28.4 |
| CIS | Cistaceae | S | 39 | 6.5 | 28 | 4.9 | 81 | 18.2 | 52 | 22.2 | 51 | 12.6 |
| | Resprouters | | 99 | 69.1 | 100 | 84.2 | 85 | 42.8 | 79 | 72.6 | 97 | 68.3 |
| | Seeders | | 85 | 27.6 | 94 | 36.9 | 33 | 7.6 | 76 | 49.4 | 81 | 32.0 |
| | Total Shrub Cover | | 99 | 76.1 | 100 | 95.1 | 96 | 60.3 | 80 | 112.7 | 99 | 87.1 |
| **N** | **species richness** | | ***mean= 7 max=19*** | | ***mean= 9 max=14*** | | ***mean= 5 max=10*** | | ***mean= 9 max=18*** | | ***mean= 7 max=19*** | |
| | | | ***Total N = 35*** | | ***Total N =40*** | | ***Total N = 24*** | | ***Total N = 52*** | | ***Total N = 64*** | |
| ERI | *Erica arborea* | R | 24 | 2.4 | 6 | 1,0 | 13 | 3.4 | 10 | 1.5 | 15 | 2.1 |
| CIS | *Cistus psilosepalus* | S | 19 | 3.2 | 4 | 1.7 | 4 | 0.2 | 8 | 1.6 | 11 | 2.0 |
| LEG | *Ulex europaeus* | R | 32 | 5.4 | 42 | 5.5 | 19 | 3.4 | 1 | 0.3 | 23 | 3.7 |
| LEG | *Pterospartum tridentatum* | R | 39 | 7.9 | 62 | 6.8 | 44 | 9.3 | 55 | 8.3 | 48 | 8.0 |
| ERI | *Calluna vulgaris* | S | 36 | 4.6 | 78 | 9.0 | 21 | 3.2 | 60 | 8.2 | 48 | 6.2 |
| ERI | *Erica umbellata* | S | 36 | 5.2 | 62 | 7.2 | 10 | 2.8 | 49 | 8.0 | 40 | 5.9 |
| ERI | *Erica ciliaris* | R | 17 | 1.2 | 52 | 7.6 | 10 | 2.1 | 0 | 0.0 | 17 | 2.1 |
| LEG | *Ulex micranthus* | R | 12 | 2.6 | 54 | 11.6 | 0 | 0.0 | 1 | 0.1 | 14 | 3.0 |
| LEG | *Genista triacanthos* | R | 9 | 0.6 | 50 | 8.2 | 2 | 0.2 | 70 | 14.0 | 32 | 5.6 |
| LEG | *Ulex minor* | R | 46 | 6.8 | 62 | 12.2 | 69 | 18.7 | 26 | 6.8 | 47 | 9.7 |
| ERI | *Erica cinerea* | S | 35 | 3.2 | 78 | 8.0 | 52 | 13.3 | 28 | 2.4 | 43 | 5.5 |
| ERI | *Erica australis* | R | 19 | 6.0 | 20 | 4.2 | 35 | 5.1 | 25 | 4.2 | 24 | 5.0 |
| LEG | *Cytisus spp.* | R | 12 | 3.2 | 2 | 1.1 | 25 | 7.8 | 6 | 2.5 | 11 | 3.4 |
| CIS | *Cistus ladanifer* | S | 1 | 0,0 | 0 | 0.0 | 25 | 5.3 | 35 | 8.3 | 14 | 3.3 |
| ROS | *Rubus ulmifolius* | R | 17 | 1.9 | 12 | 3.0 | 10 | 2.0 | 36 | 6.4 | 20 | 3.4 |
| BOR | *Lithodora prostrata* | R | 4 | 0.3 | 22 | 1.2 | 0 | 0.0 | 51 | 4.5 | 20 | 1.6 |
| CIS | *Cistus monspelienses* | S | 0 | 0.0 | 6 | 0.6 | 0 | 0.0 | 33 | 7.3 | 10 | 2.2 |
| LEG | *Ulex airensis* | R | 0 | 0.0 | 2 | 0.1 | 0 | 0.0 | 25 | 5.4 | 7 | 1.5 |
| LAB | *Lavandula spp.* | S | 1 | 0.4 | 0 | 0.0 | 0 | 0.0 | 24 | 3.4 | 7 | 1.1 |
| CIS | *Cistus salviifolius* | S | 2 | 0.4 | 8 | 1.2 | 0 | 0.0 | 14 | 2.4 | 6 | 1.0 |
| CIS | *Halimium ocymoides* | S | 1 | 0.2 | 2 | 0.5 | 6 | 0.5 | 14 | 1.7 | 6 | 0.7 |
| LEG | *Ulex jussiaei* | R | 0 | 0.0 | 6 | 2.0 | 0 | 0.0 | 15 | 2.5 | 5 | 1.0 |
| OLE | *Phillyrea angustifolia* | R | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 19 | 2.1 | 5 | 0.6 |
| ERI | *Arbutus unedo* | R | 1 | 0.4 | 2 | 0.2 | 2 | 0.8 | 11 | 2.0 | 4 | 0.9 |

Very rare species are not listed, but are included in the functional groups and specific richness. Grey shaded cells refer to the most characteristic species of each region, reflected by the higher frequency than observed for the totality of the plots. Families: ERI – Ericaceae, CIS – Cistaceae, LEG – Leguminosae/Fabaceae, ROS – Rosaceae, BOR – Boraginaceae, OLE – Oleaceae. Reg (post-fire regeneration strategy recognized in the field) – R – obligate or facultative resprouter, S – obligate seeder.

*Species richness includes all woody species regenerating in the understory, including native trees, pines and eucalypts.

# Chapter 6

# General Discussion

# and Main Conclusions

# Chapter 6

# General Discussion and Main Conclusions

## 6.1. Fire-related germination response of the main study species

### 6.1.1. Facultative resprouters

The germination of *Erica australis* seeds from a population from Central Portugal was substantially increased after exposure to 100ºc for 5min (Vasques et al. 2012), while a study from northeast Spain had a comparatively smaller increase in germination percentage, and a comparatively higher germination percentage in the control (Valbuena & Vera, 2002). (**Figure 17**-inset). There is great variability between the populations studied, both in terms of the germination from the control samples, as in relation to the enhancement caused by exposure to similar heat treatments.

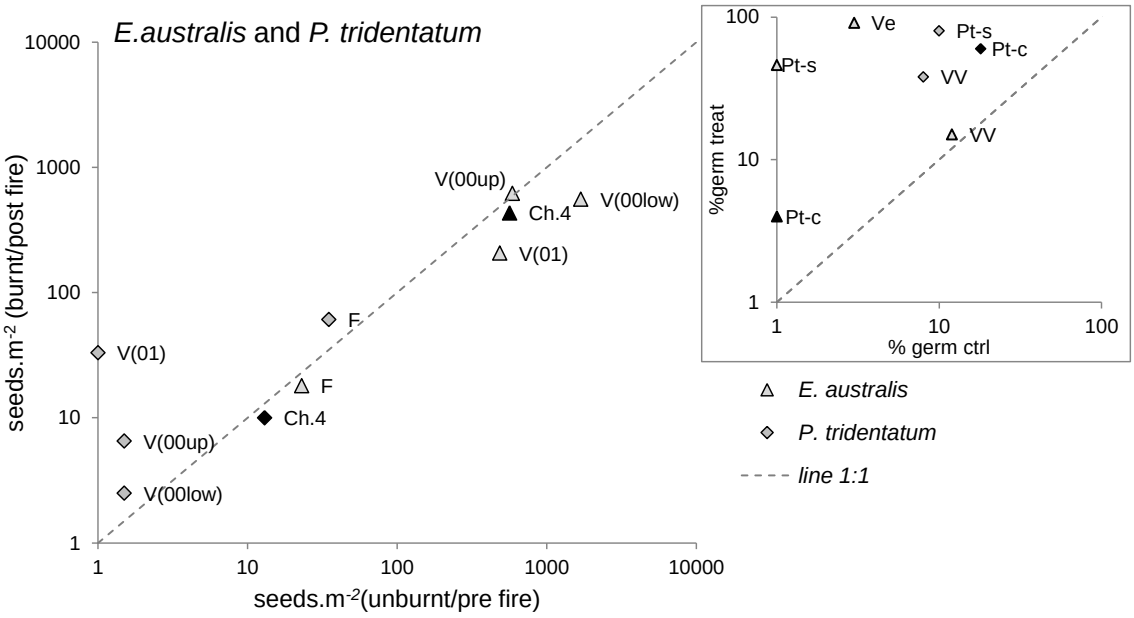



**Figure 17** - Fire-induced differences in density of germination of *Erica australis* (triangles) and *Pterospartum tridentatum* (diamonds) from the soil seed bank (main figure) and differences in germination percentage as induced by heating exposure, under laboratory conditions (inset). Black dots are results from populations of Central Portugal. Main figure: V00 – Valbuena et al. 2000; up – 0-2 cm; low – 2-5 cm, V01 – Valbuena et al., 2001, F – Fernández et al., 2013 Ch. 4 – Maia et al, (in prep). Inset:, or similar. Pt – Vasques et al., 2012 (100ºC 5min); c – central Portugal provenance, s – south Portugal provenance, Ve – Vera et al., 2010 (110ºC 10min), VV – Valbuena & Vera, 2002 (100º 4min).

However, despite the variability in germination response after heat exposure, the post-fire induced changes in the germination from the soil seed bank were not so marked by population differences (**Figure 17**). Moreover, most of the data points appear slightly under the 1:1 line, indicating a minor but notwithstanding consistent negative overall effect of fire in the germination ability of this species.

For *P.tridentatum*, a legume facultative resprouter, germination was stimulated after heat exposure in a more consistent way, among different Portuguese and Spanish populations (**Figure 17**- inset). The germination response from the soil samples is more variable – while studies from North Spain show an increase in

the germination densities after fire, the results from the experimental fire in central Portugal (Ch. 2) indicate a slight decrease after fire. In any of the studies, the germination densities from the soil seed bank samples were very low when compared with *E.australis*, even when *P. tridentatum* was the dominant species in the above ground vegetation (Ch.4). The exception to this was the study by Fernández, et al. (2013), that showed lower germination density of *E. australis* and higher density of *P. tridentatum* than any of the other studies.

However, the indirect method for evaluating the seed bank in Chapter 4 does not permit definitive conclusions as to the actual soil seed bank densities of *P. tridentatum*. In the case that temperatures achieved by fire in the soil were lower than the temperature required to stimulate its germination, the post-fire germination densities would simply be the result of lack of stimulation. In this case, the lack of significant differences with the pre-fire samples could not be explained by low pre-fire seed densities. In any case, this alternative explanation for the post-fire low germination of *P. tridentatum* does not seem very likely, since the same temperatures attained by the experimental fire were significantly related with fire-induced changes in the germination of *E. australis* seeds, even if the net result, at the slope scale was a (non-significant) decrease (**Figure 17**, main) (Ch. 4). Also, the results of this study are not discrepant with others reported in the literature (references from Figure 1).

### 6.1.2. Obligate seeders

*Calluna vulgaris* was one of the dominant *taxa* germinating from the soil seed bank of a *Pinus pinaster* forest, after a wildfire (Ch. 2, Ch. 3). Its post-fire germination density was higher after fire, but the post-fire enhancement was more preeminent in the patches with low fire severity than in the ones with high fire severity, indicating that the higher temperatures attained by fire would damage the seeds. The germination of this species after an experimental fire in North Spain has reported lower differences from the pre-fire situation, while reporting higher densities from the unburnt samples (Luz Valbuena et al. 2000). A laboratory trial on the effect of temperature on the germination percentage of *Calluna vulgaris*, using seeds collected in North of Spain (Gonzalez-Rabanal & Casal 1995) showed no differences in the germination percentages of the control and the treated seeds, which agrees with the limited response of this species to temperatures caused by fire, in the populations of North Spain studied by Valbuena et al. (2000).

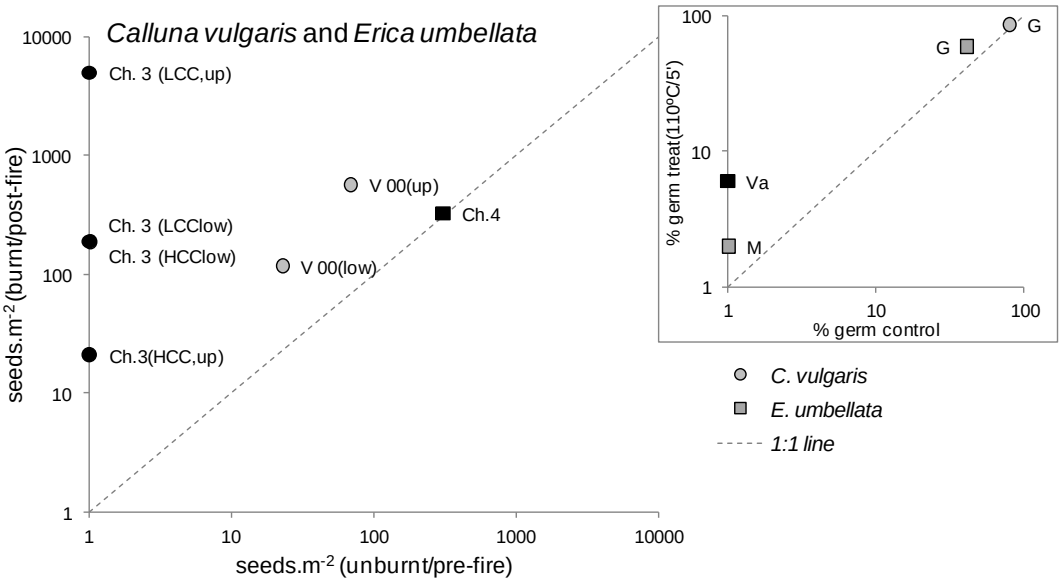



**Figure 18** – Fire-induced differences in density of germination of *C.vulgaris* (circles) and *E. umbellata* (triangles) from the soil seed bank (main figure) and differences in germination percentage as induced by heating exposure, under laboratory conditions (inset). Black dots are results from populations of Central Portugal. Main figure: V00 – Valbuena et al. 2000; up – 0-2 cm; low – 2-5 cm. Ch. 3 – Maia et al, 2012a; LCC/HCC – Low Crown pine Consumption (surrogate of fire severity)up - 0-3 cm; low -3-6cm., incluir low severity and high severity Inset: M- Moreira et al., 2010 (100ºC 5min), Va – Vasques et al., 2012 (100ºC 5min), G – González-Rabanal & Casal, 1995 (110ºC 10min).

The various results of *Erica umbellata* seeds consistently showed increased germination percentage after exposure to heat in laboratory trials, among studies and populations (**Figure 18**-inset). Although the degree of enhancement of germination percentage was different amongst populations, the biggest difference was found in the percentage of germination of the untreated seeds. Moreover, the study that showed higher percentage of germination in the control also showed the lesser increase in germination response after heat exposure, given by the smallest distance to the 1:1 line (Gonzalez-Rabanal & Casal 1995). Actually, the data in **Figure 18** shows, not only a decrease in germination percentage in unheated seeds from northern to southern populations, but at the same time, an increase in the heating stimulus to

germination along the north-south gradient. This might be related to historical fire-related pressures on these regions, which probably lead to fire free regeneration to be a bigger advantage in the northern areas, less affected by fire, than in the south, where post-fire regeneration ability is likely to be more important for population persistence (Vasques et al. 2012).

*Calluna vulgaris* is considered an obligate seeder in the Iberian peninsula (L Calvo et al. 2005; Paula & J. G. Pausas 2008). The role of fire in shaping the regeneration mechanisms of this species has been questioned (J G Pausas et al. 1999), since *Calluna vulgaris* germinates after many disturbance types (e.g. Calvo, Tarrega, & Luis, 2002). In fact, the laboratory and seed bank results of (Gonzalez-Rabanal & Casal 1995; Luz Valbuena et al. 2000), respectively, confirm the limited stimulus caused by high temperature on this species. The results presented in Chapter 4 (**Figure 13**) show that, also in the case of *E. umbellata* germination does not occur exclusively post-fire, indeed, pre-fire and post-fire germination densities are similar. This supports that, like in the case of *Calluna vulgaris*, and other obligate seeders in the Mediterranean basin (Santana et al. 2013) fire might have been one of several disturbances shaping germination response.

### 6.1.3. *Pinus pinaster*

After sexual maturity, cone serotiny is the ultimate limiting factor of *Pinus pinaster* postfire regeneration, as it determines seed availability. There are evidences that fire history has a fundamental role in the expression of the degree of serotiny in *P. pinaster* (Hernández-Serrano et al. 2013). However,

plantations have a great weight in the area of the distribution of this species in Portugal, which challenges the generalization of these relations to Portuguese pine forests.

**Figure 19** supports that potential post-fire pine regeneration density, is partially a result of the density of mature trees, (Moya, et al., 2008). The plot shows a consistent trend towards increased pine seedling densities with increasing density of mature trees, and at the same time, an increase in pine recruitment from unburnt sites to intermediate canopy damage, which decreases with increasing canopy damage (unaffected to scorched to torched). In this context, it may be assumed that if, in some portions of the pine forest studied in Chapter 2, fire was restricted to the understory and the canopies had not been directly affected by the flames, the pine regeneration densities would have been higher. This type of fire behaviour is in agreement with low severity prescribed burning that envisage the diminishing of fuel loads without causing mortality of the trees ( Fernandes et al. 2013; Fernandes & Botelho 2004) .

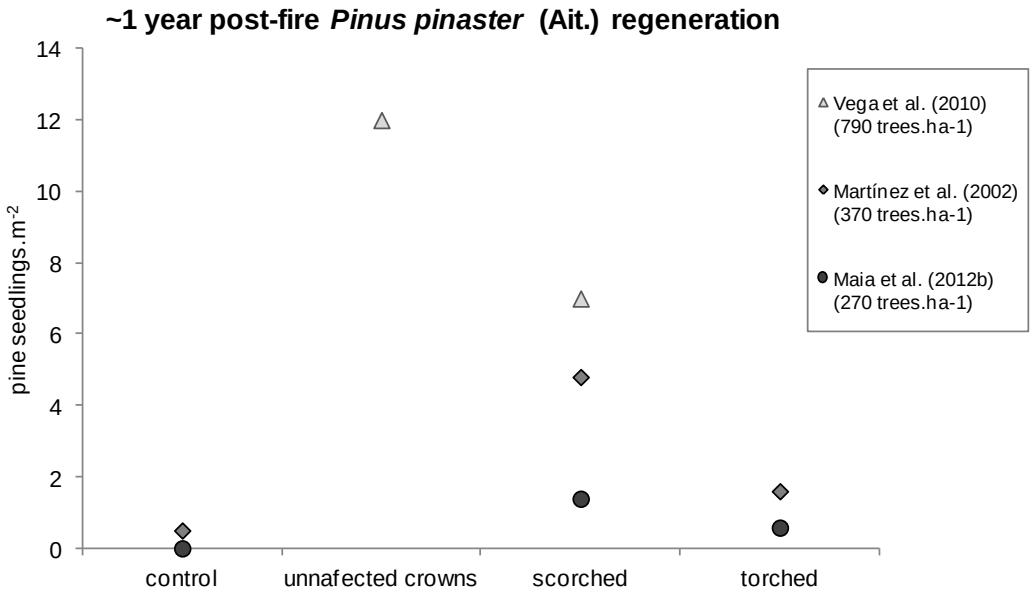



**Figure 19** - Post fire recruitment density of *Pinus pinaster*,approximately one year after fire, for different chategories of fire-induced damage to the canopies. Density of mature trees is given in the figure legend.

While post-fire seed rain seems to be mostly controlled by the canopy seed bank in relation to the fire severity in the crowns, pine seedling establishment patterns also depend on post-fire soil conditions. These conditions may be directly related to fire severity on the soil surface, like nutrient changes, litter and duff combustion, pH (J.G. Pausas et al. 2004; J G Pausas et al. 2003; Madrigal et al. 2010; Saracino et al. 2002), but also indirectly related to fire-induced crown damage, which influences the post-fire litter fall (Ch. 2). This indicates that in the case that post-fire soil conditions are not favourable, fire-induced damage to the crown is, *per se* a poor indicator of post-fire potential for pine recruitment (Vega et al. 2008, *cf*. Chapter 2). In Chapter 2, however, the degree of combustion of the pine trees, proved to be a good surrogate of the potential for post-fire pine recruitment in a burnt mature *P. pinaster* forest, in

agreement with the previous studies of Vega et al. (2010) and Martínez et al, (2002).

The evaluation of the potential for the pine forest to self-regenerate has applicability in the planning of post-fire forest plans towards forest conversion, or on the contrary, to expect post-fire tree regeneration. Wildfires are a driver of forest conversion into eucalypt plantations (Silva et al. 2011), even in the presence of abundant post-fire pine regeneration (personal observation). However, if carefully planned, such practices could be avoided, with higher economic gain (natural regeneration does not imply economic investment), potentially less soil (fertility) losses and hence higher compliance with forest sustainability criteria (FSC 2012). The correct evaluation of the effects of fire is most useful, in the sense that it may allow managers to direct the logistical and economical efforts towards areas with more probability of decreased ability of post-fire regeneration of the main tree species.

### 6.2. Combined effects of fire and management in the community dynamics

#### 6.2.1. Heathands and shrub communities of Pine and Eucalypt plantations

*Pterospartum tridentatum* and *Erica australis* are strong post-fire resprouters, so that the contribution of the seedlings to the post-fire community is not expected to be the dominant mechanism for population persistence. In fact, in a recent study, Céspedes et al., (2014) have classified *E. australis* as an obligate resprouter, supposedly by not being able to find any seedlings of this species after fire.

In any case, both *E. australis* and *P. tridentatum* have the ability to regenerate from seeds after a fire (Figure 2; references within), which provides them with the possibility to maintain their populations, even under scenarios that lead to decreased (or loss of) resprouting ability (*sensu lato*, *i.e.*, also including survival of sprouts- (Moreira et al. 2012). like after repeated fires or after ploughing (Ch. 5).

However, there are severe limitations to the importance of germination as a persistence mechanism (of obligate resprouters) under recurrent disturbance conditions. It is unlikely that a disturbance scenario would decrease the resprouting ability without affecting the production of seeds, particularly in the case of *E. australis* ('no allocation trade-offs' - Cruz & Moreno 2001). This type of scenario would require fire return intervals short enough to deplete the underground reserves, but still long enough to allow for seeds production.

Even under 'normal disturbance' regimes, the contribution of germination to post-fire recovery of these species is low. This is because 1) the resprouting vigour of these two species is so high that they would rapidly become the dominant species in heathland communities. Also, 2) the seed density is higher under the canopies of the mother-plant, at least in the case of *E. australis* (Ch.2). As a result, the intraspecific competition with the resprouting shrubs is higher in the location where more propagules are available for recruitment.

In the case of *Erica umbellata* and *Calluna vulgaris*, the post-fire seedling recruitment and establishment should be more constrained by inter- than by intra-specific competition (if the autohinibition of the litter is not a significant factor (Bonanomi et al. 2005). Seed deposition rates are higher under the canopy of *E. umbellata* (Ch. 4) and also for *Calluna vulgaris* there are

evidences of higher deposition rates at short distances from the mother plant (Gilbert & Butt 2010). Since adult shrubs are killed by fire, there is no competition for resources with the mother plant in the locations with higher probability of seedling recruitment. In this context, the abundance of these species prior to disturbance is also an important condition for the success of effective post-fire regeneration. In any case, the success of seedling establishment may be quite limited, and severely constrained by the season of fire, due to the probabilities of rain in the early germination phases (Quintana et al. 2004).

When these seeder species co-exist with strong resprouters, they may be rapidly outcompeted due to their conspicuous vegetative regeneration. As a consequence, there is the possibility for a progressive displacement of obligate seeders in these communities. In fact, that may be the reason for the much lower abundances of *E. umbellata* in relation to *E. australis* and *P. tridentatum* in the above ground of the heathland studied in Ch. 4. However, more research is needed to validate this supposition.

In the case of *P.tridentatum*, the soil seed bank seems to be rather limitative for post-fire seed recruitment, as seed densities in the soil seed bank are very low (Ch.4). Methodological constraints regarding the technique used to evaluate the seed bank of the heathland (Ch.4) more precisely, the fact that it was only evaluated through the observation of the emerging seedlings (indirect method) rather than in combination with the direct observation of the seeds contained in the soil - did not allow unequivocally attributing the low post-fire germination of *Pterospartum tridentatum* to correspondingly pre-fire seed densities. Although some suggestions were made to explain this phenomenon, as pre-dispersal

predation by pod infestation or post dispersal transport by ants (Podlussány et al. 2001; Lopez 2000; Hughes & Westoby 1990), evaluating these ecological processes was beyond the framework of this thesis. The study of Fernández et al. 2013 showed different results, in terms of the seed bank of P. tridentatum – much higher densities (10 fold) and even a significant increase in germination density after fire. Further research may enlighten on the existence and importance of such ecological processes in populations of *P. tridentatum,* and therefore elucidate if they may be a reason behind the discrepancies between the results of Chapter 4 and those of Fernández et al., 2013.

One of the implications of having a small soil seed bank of is that, in the case of loss of vegetative vigour, the persistence of *P. tridentatum* would depend on the production of seeds immediately before disturbance (assuming that they escape predation). In fact, this is what happens with “in season” summer fires that burn after the dispersion of *P. tridentatum* seeds in late-spring early-summer. In the case of *E. australis* the recent flower production (in the same year as the disturbance) would not be so limiting for post-disturbance recruitment as in the case of *P. tridentatum*, since it builds an abundant permanent seed bank that compensates the eventual low seed production in the same year (Bossuyt & Honnay 2008).

The density of the main species in the soil seed bank was linked to the position under the canopy of the dominant shrubs. This was particularly strong in the case of *Erica australis*, although there were also evidences of the same for the obligate seeder *E. umbellata* (not statistically significant, probably due to low sample numbers). While not completely unexpected, it highlights the importance of the sampling location in the assessment of community soil seed banks. In

this sense, an accurate sampling scheme for analysing the soil seed bank of dense shrubland communities, in terms of seed density and species composition, could be based in a hierarchical approach, distributing the sample numbers, not only between shrub patches and gap areas (Torres et al. 2013), but moreover, by re-distributing the samples assigned to shrub patches under the canopies of the different shrub species.

In the pine forest studied in Ch. 2, the regeneration of the understory vegetation by resprouting was not related with contrasting fire severity, supporting the limited potential of severity indices in predicting post-fire resprouting (Keeley 2009). A recent study in North Spain has addressed the role of fire severity in the of post-fire resprouting vigour of *E. australis* and *P. tridentatum* (Fernández, José A. Vega, et al. 2013). They have showed a significant impact of fire in the resprouting vigour of these two species, however limited to a short period after fire. The results of Moreira, Tormo, and Pausas (2012) show other factors playing a role in the ability to regenerate vegetative; particularly relevant is the amount of stored reserves, constrained by previous disturbance regime. In this context, the ability to regenerate after other disturbances, like post-fire management shrub clearing would also depend on the recurrence of disturbances (fire and management related).

The effect of post-fire management has, indeed shown to be an important factor constraining the cover of resprouters in the understory of monospecific plantations (Ch. 5). Moreover, this effect was more pronounced in areas with overall lower plant cover, indicating that the pre-disturbance condition of the community is an important factor to consider.

The understory cover assessment on Chapter 2 was not done at specific timing to allow the impact of post-fire logging on the understory regeneration and in any case, the visible perturbation in the study plots was negligible. However, it was possible to observe that wood extraction was not limited to the pine trees, many burnt branches of big shrubs like *Arbutus unedo* and *E. australis* were also cut, simply as a way of smoothing the progress of the work. This is probably one of the reasons for the negative impact of tree harvest on the shrub communities of Pine and Eucalypt plantations (Ch. 5), i.e. the understory layer is affected by side effects of the management.

Soil mechanical disturbances have a more deterministic effect on resprouting shrubs. After soil tilling, many of the resprouters are killed, due to uprooting or, at least, severely damaged. Contrastingly, the regeneration of post-fire seeders did not seem to be affected by this operation, at least in the mid-term, which is agreement with a faster post-disturbance recovery than resprouters (Lamont and Wiens, 2003).

Fire can decrease the vegetative vigour of resprouter species, which turns fire into a potential tool for the conservation of endangered seeder species (Pyke et al. 2010), particularly if they are strongly stimulated by fire (Vaughton 1998; Yates & Ladd 2010). Since the germination of *Erica umbellata* and *Calluna vulgaris* in the communities of study does not seem to be strongly stimulated by fire (soil seed bank samples, Ch. 2 and 3), the hypothetical use of fire, alone, as a tool for the restoration of these populations is of limited interest. Resprouter species are more sensitive than seeders to forest management practices that involve soil disturbance (Ch. 5 Maia et al. 2014), since, unlike fire, mechanical soil preparation operations directly damage the roots. In this way, the combined

use of fire and soil mechanical preparation-based techniques could be of interest for allowing the colonization of locally endangered seeder species, by lowering inter-specific competition with resprouters. Unquestionably, the hypothetical application of these operations must be planned with extreme caution, since they carry associated risks (e.g. increased risks of soil (fertility) loss, Malvar, PhD Thesis, 2013; Martins et al. 2013). In any case, the application of management techniques to the conservation of seeder species is not suggested for any of the communities of study; to the present there are no evidences of local extinction of seeder shrub populations (all chapters), even in heathlands dominated by resprouters (Ch.2).

### 6.2.2. Pine forests

The complexity in post-fire pine regeneration patterns may increase with post-fire management in the area, since the timing of management is crucial in the effect it has on seedling mortality ( Vega et al. 2008; Vega et al. 2010; Fernandez et al. 2008). In Chapter 4, post-fire management was inevitably included in the study, as a disturbance affecting all the study slope after the 6$^{th}$ month post-fire. The mortality caused by management operations caused a decrease in pine density in both types of fire severity patches, but more pronounced in the case of the Low Crown Consumption (LCC) patches, mostly due to higher initial seedling densities. After this disturbance, a second pulse of germination increased seedling density, but mostly on the LCC patches. This second pulse of germination was linked to increased cone density in the ground, likely an indication of seed rain fostered by pine logging.

As was mentioned in relation to the timing of tree harvest in the regeneration of the understory community of this a study site, pine regeneration could be more affected if tree harvest had occurred at a later stage (Vega et al. 2008). This would be especially limiting in terms of pine regeneration if harvesting had occurred after the second pulse of germination, since the possibility of further recruitment would be severely limited.

The post-fire density of pine seedlings was not found to be related with the regeneration of the understory vegetation during the first 36 months after fire (Ch. 2). While this was probably related to the somewhat low density of pine seedlings, as well as of low cover of the understory layer, it can also be attributed to favorable climate, since more arid regions show higher degree of inter-specific competition (J G Pausas et al. 2003). This makes evident that the effectiveness of management operations to reduce competition with the trees is more limited in productive regions where resources availability is higher. Management operations that consist of shrub removal show a higher impact in shrub cover in less productive regions (Ch.5). Therefore, this indicates that the putative effect in terms of reducing competition with the pines is higher in such areas. On the other hand, the effects of such operations at the long term are potentially more damaging in vulnerable areas (e.g. steeper slopes), particularly in what concerns the lower regeneration of plant cover and the implications thereof in terms of soil protection. This implies that the creation of global principles for the sustainable management of pine forests is impracticable. The biogeographic setting and topography (Ch. 5) should be taken into consideration, thoroughly analyzing the dynamics of interspecific competition and facilitation (Simard et al. 2006; Harrington 2006). In spite limited resources

may promote higher competition in harsh environments, facilitation is also more important in harsher environments (e.g. (Callaway et al. 1996).

### 6.3 Conclusions

The results of this thesis allowed answering to the main objectives. The main conclusions of the work presented in this thesis, regarding post-fire vegetation regeneration with potential implications for management are the following:

1- Fire severity, as estimated by the degree of Crown Consumption (LowCC or HighCC) as well as by other severity indices related to soil surface properties (ash and litter covers) and twig diameters (TSI), was as a key factor in post-fire pine recruitment. Pine seedlings density was significantly higher following lower (LCC) than higher (HCC) fire severity, and could be significantly predicted by TSI.

2- From the severity indices studied, both crown consumption and TSI were significant predictors of post-fire pine recruitment density. The cover by needles was also a good predictor of the recruitment density. The degree of needle cover could, moreover be easily predicted by the Crown Consumption classes, as justified by the logical as well as statistical link between litter cover and needle cast from scorched crowns. This highlights the degree of canopy damage as a valuable “visual tool” for predicting P. pinaster post-fire regeneration potential.

3- Fire increased the germination from the soil seed bank of a *Pinus pinaster* forest. The densities of seedlings of the dominant *taxa* (genus *Erica* and *Calluna vulgaris*) were contrastingly affected in relation to the unburned situation – a germination increase was observed in the plots with LCC, and a decrease in the plots with HCC.

4- The severity index based on the diameters of remaining twigs (TSI) could explain the marked variability in viable seed densities between the LCC and HCC patches. However, the use of MTR (Maximum Temperature Reached) estimations by NIR (Near Infrared Spectroscopy) was not useful to predict germination from the soil seed bank, neither within nor between the patches with different crown consumption degrees.

5- An experimental fire conducted in a heathland did not result in net differences in germination from the soil seed bank. However, the variability in maximum temperatures recorded at 1,5 cm in the soil (28 -74.5ºC) caused divergent effects over the burned plot in terms of *Erica australis* germination – a progressive increased was observed in the plots were maximum temperature recorded ranged from 29 to 42.5ºC and decreased in plots with maximum temperature ranging from 51.5 to 74.5ºC

6- The density of *E. australis* soil seed bank was significantly higher under its canopy, and the same was suggested for *E. umbellata*. Contrarily, the density of *P. tridentatum* seeds was similarly low under its canopy or under the other shrubs. The post-fire germination from the soil seed bank followed the same trend. Methodological constraints regarding the technique used to evaluate the seed bank of the heathland more precisely, the fact that it was only evaluated through the observation of the emerging seedlings (indirect method) rather than in combination with the direct observation of the seeds contained in the soil - did not allow unequivocally attributing the low post-fire germination of *P. tridentatum* to correspondingly pre-fire seed densities.

7- From the indirect assessment of the soil seed bank, it cannot be confirmed that *E. umbellata* population are in risk of local extinction. Despite the low relative abundance and cover of *E. umbellata* shrubs in the community, its seed shadow went far beyond the location of the adult shrubs. Nonetheless further investigation should be done on the *in situ* establishment of *E. umbellata*, to verify these assumptions in the mid to long-term post-fire.

8- Biogeographic region was the main factor determining the richness and abundance of woody species of the understory of pine and eucalypt plantations. Topography was a significant factor in determining species richness; woody species richness increased with increasing slope angle. Overall, post-fire tree harvest, shrub clearing and soil tilling showed negative effects in the mid-term cover attained by resprouters, but soil tilling did not affect seeders in a significant way.

9- The negative effect of post-fire management actions on vegetation was dependent on the region where it took place. Vulnerable regions exhibited stronger management impacts than more productive regions, even with less management pressure.

## References (of the Discussion and Conclusions)

Bonanomi, G., Legg, C. & Mazzoleni, S., 2005. Autoinhibition of germination and seedling establishment by leachate of Calluna vulgaris leaves and litter. Community Ecology, 6(2), pp.203–208.

Bossuyt, B. & Honnay, O., 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. Journal of Vegetation Science, 19(6), pp.875–884.

Callaway, R.M. et al., 1996. Competition and Facilitation: Contrasting Effects of Artemisia Tridentata on Desert vs. Montane Pines. Ecology, 77(7), pp.2130–2141.

Calvo, L. et al., 2005. Differences in the response to fire of Mediterranean shrubland. In New Research on Forest Ecosystems. pp. 21–36.

Calvo, L., Tarrega, R. & Luis, E., 2002. Regeneration patterns in a Calluna vulgaris heathland in the Cantabrian mountains (NW Spain): effects of burning, cutting and ploughing. Acta Oecologica, 23(2), pp.81–90.

Cruz, A. & Moreno, J.M., 2001. No allocation trade-offs between flowering and sproutingin the lignotuberous, Mediterranean shrub Erica australis. Acta Oecologica, 22(2), pp.121–127.

Fernandes, P. & Botelho, H., 2004. Analysis of the prescribed burning practice in the pine forest of northwestern Portugal. Journal of Environmental Management, 70(1), pp.15–26.

Fernandes, P.M. et al., 2013. Prescribed burning in southern Europe: developing fire management in a dynamic landscape. Frontiers in Ecology and the Environment, 11(s1), pp.e4–e14.

Fernandez, C. et al., 2008. Effects of wildfire, salvage logging and slash manipulation on Pinus pinaster Ait. recruitment in Orense (NW Spain). Forest Ecology and Management, 255(3-4), pp.1294–1304.

Fernández, C., Vega, J. a & Fonturbel, T., 2013. Fuel reduction at a Spanish heathland by prescribed fire and mechanical shredding: effects on seedling emergence. Journal of environmental management, 129, pp.621–7.

Fernández, C., Vega, J.A. & Fonturbel, T., 2013. Does fire severity influence shrub resprouting after spring prescribed burning? Acta Oecologica, 48, pp.30–36.

Forest, C.F.O.R., 2012. Forest Stewardship Council - FSC Principles and Criteria fos Forest Stewardship. Available at: http://www.fsc.org/en/about/policy_standards/princ_criteria.

Gilbert, J.A. & Butt, K.R., 2010. Dispersal of Calluna vulgaris ( L .) Hull . seeds on severely burnt upland moorland. , 6(2000), pp.1–6.

Gonzalez-Rabanal, F. & Casal, M., 1995. Effect of high temperatures and ash on germination of ten species from gorse shrubland. Vegetatio, 116(2), pp.123–131.

Harrington, T., 2006. Plant Competition, Facilitation, and Other Overstory-Understory Interactions in Longleaf Pine Ecosystems. In S. Jose, E. Jokela, & D. Miller, eds. The Longleaf Pine Ecosystem SE - 5. Springer Series on Environmental Management. Springer New York, pp. 135–156.

Hernández-Serrano, A. et al., 2013. Fire structures pine serotiny at different scales. American journal of botany, 100(12), pp.2349–56.

Hughes, L. & Westoby, M., 1990. Removal rates of seeds adapted for dispersal by ants. Ecology, 71(1), pp.138–148.

Keeley, J., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire, 18(1), p.116.

Lopez, J., 2000. Production and morphology of fruit and seeds in Genisteae (Fabaceae) of south-west Spain. Botanical Journal of the Linnean Society, 132(2), pp.97–120.

Madrigal, J. et al., 2010. Smouldering fire-induced changes in a Mediterranean soil (SE Spain): effects on germination, survival and morphological traits of 3-year-old Pinus pinaster Ait. Plant Ecology, 208(2), pp.279–292. Available at: <Go to ISI>://000277182100009.

Maia, P. et al., 2012. Wildfire effects on the soil seed bank of a maritime pine stand — The importance of fire severity. Geoderma, pp.1–9.

Martins, M. a. S. et al., 2013. Runoff and inter-rill erosion in a Maritime pine and a Eucalypt plantation following wildfire and terracing in north-central Portugal. Journal of Hydrology and Hydromechanics, 61(4), pp.261–268.

Moreira, B., Tormo, J. & Pausas, J.G., 2012. To resprout or not to resprout: factors driving intraspecific variability in resprouting. Oikos, 121(10), pp.1577–1584.

Paula, S. & Pausas, J.G., 2008. Burning seeds: germinative response to heat treatments in relation to resprouting ability. Journal of Ecology, 96(3), pp.543–552.

Pausas, J.G. et al., 2003. Fire severity and seedling establishment in Pinus halepensis woodlands, eastern Iberian Peninsula. Plant Ecology, 169(2), pp.205–213.

Pausas, J.G. et al., 1999. Post-fire regeneration patterns in the eastern Iberian Peninsula. Acta Oecologica-International Journal of Ecology, 20(5), pp.499–508.

Pausas, J.G., Ribeiro, E. & Vallejo, R., 2004. Post-fire regeneration variability of Pinus halepensis in the eastern Iberian Peninsula. Forest Ecology and Management, 203(1-3), pp.251–259.

Podlussány, A., Jermy, T. & Szentesi, Á., 2001. On the leguminous host plants of seedpredator weevils (Coleoptera: Apionidae, Curculionidae) in Hungary. Acta Zoologica Academica Scientarium Hungaricae, 47(4), pp.285–299.

Pyke, D. a., Brooks, M.L. & D'Antonio, C., 2010. Fire as a Restoration Tool: A Decision Framework for Predicting the Control or Enhancement of Plants Using Fire. Restoration Ecology, 18(3), pp.274–284.

Quintana, R. et al., 2004. Time of germination and establishment success after fire of three obligate seeders in a Mediterranean shrubland of central Spain. , pp.241–249.

Santana, V.M., Baeza, M.J. & Blanes, M.C., 2013. Clarifying the role of fire heat and daily temperature fluctuations as germination cues for Mediterranean Basin obligate seeders. Annals of botany, 111(1), pp.127–34.

Saracino, A. et al., 2002. Pattern of resin dripping under Aleppo pines (Pinus halepensis Mill.) of different crown size. Fire and Biological Processes, pp.291–301.

Silva, J.S. et al., 2011. Wildfires as a major driver of landscape dynamics in three fire-prone areas of Portugal. Landscape and Urban Planning, 101(4), pp.349–358.

Simard, S.W. et al., 2006. Evidence for competition and facilitation trade-offs: effects of Sitka alder density on pine regeneration and soil productivity. Canadian Journal of Forest Research, 36(5), pp.1286–1298.

Torres, I. et al., 2013. Spatial relationships between the standing vegetation and the soil seed bank in a fire-prone encroached dehesa in Central Spain. Plant Ecology, 214(2), pp.195–206.

Valbuena, L., Tárrega, R. & Luis-Calabuig, E., 2000. Seed banks of Erica australis and Calluna vulgaris in a heathland subjected to experimental fire. Journal of Vegetation Science, 11, pp.161–166.

Valbuena, L. & Vera, M.L., 2002. The effects of thermal scarification and seed storage on germination of four heathland species. , pp.137–144.

Vasques, A. et al., 2012. Germination in five shrub species of Maritime pine understory—does seed provenance matter? Annals of Forest Science, 69(4), pp.499–507.

Vaughton, G., 1998. Soil seed bank dynamics in the rare obligate seeding shrub, Grevillea barklyana (Proteaceae). Australian Journal of Ecology, 23(4), pp.375–384.

Vega, J.A. et al., 2010. Response of maritime pine (Pinus pinaster Ait.) recruitment to fire severity and post-fire management in a coastal burned area in Galicia (NW Spain). Plant Ecology, 206(2), pp.297–308.

Vega, J.A. et al., 2008. The influence of fire severity, serotiny, and post-fire management on Pinus pinaster Ait. recruitment in three burnt areas in Galicia (NW Spain). Forest Ecology and Management, 256(9), pp.1596–1603.

Yates, C.J. & Ladd, P.G., 2010. Using population viability analysis to predict the effect of fire on the extinction risk of an endangered shrub Verticordia fimbrilepis subsp fimbrilepis in a fragmented landscape. Plant Ecology, 211(2), pp.305–319.